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Productivity and physical condition of white-tailed deer in New Hampshire

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PRODUCTIVITY AND PHYSICAL CONDITION OF WHITE-TAILED DEER IN NEW HAMPSHIRE

BY

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THESIS

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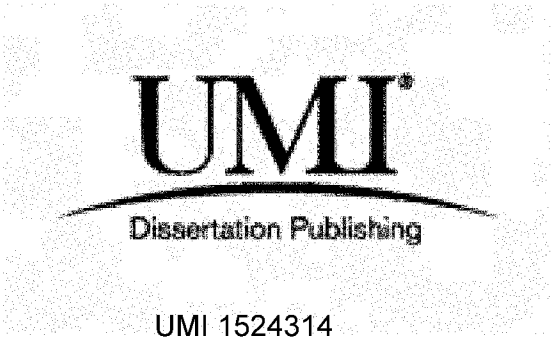

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ABSTRACT

PRODUCTIVITY AND PHYSICAL CONDITION OF WHITE-TAILED DEER IN NEW HAMPSHIRE

By

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University of New Hampshire, September 2013

This study assessed productivity and nutritional condition of deer in New Hampshire, and physical condition, productivity, and recruitment in northeastern North America. In New Hampshire, few fawns bred, but pregnancy rate and productivity of older deer were high and stable since the 1980s, despite substantially higher population density. Productivity increased due to a higher proportion of adults in 2011-2013; however, recruitment declined steadily suggesting that summer fawn mortality has increased. Nutritional condition declined throughout winter, and regardless of winter severity, most deer had depleted energy reserves and were in poor condition after April1. These findings emphasize the need to consider the timing and length of severe winter conditions when interpreting a winter severity index. Similar patterns of stable productivity and physical condition, and declining recruitment were also observed regionally.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) are an important ecological, recreational, and economic resource in New Hampshire, but recently, managers have had difficulty achieving regional population objectives. Effective management of deer populations requires reliable estimates of population parameters and historically, these parameters have been based on readily available data from legally harvested deer. Although these data are informative and easily obtained, they only provide an index of population health and productivity and are restricted seasonally.

The relationship between condition and density is well established (McCullough 1979), and deer managers often rely on variation in physical parameters such as body weight and antler measurement as indicators of herd health. New Hampshire's current deer management system incorporates reproductive data derived from studies conducted by the New Hampshire Fish and Game Department (NHFG) in the late 1970s and early 1980s and data from harvested deer collected annually at biological check stations. Deer densities have increased substantially since the 1980s and measures of productivity from harvested deer (i.e., fawns per doe and fall lactation rates) have consistently declined. Conversely, yearling antler beam diameter (YABD) and other physical condition measures have not changed (unpublished data, NHFG).

This seeming contradiction between stable YABD and declining productivity indices is of concern to managers. Increasing population density and stable physical condition measures indicate a population with high nutritional condition, whereas declining lactation rates and fawn:doe ratios indicate a population with low recruitment.

Physical measures may be unreliable for low density populations on poor sites because most of the density dependent response occurs as the population nears carrying capacity (McCullough 1999); direct measurement of productivity might provide a more sensitive index of declining habitat quality as population density increases (Verme and Ullrey 1984, Keyser et al. 2005a). Increased predation on fawns may also be occurring and could provide a simple explanation for decline in recruitment to fall. Populations of eastern coyote (*Canis latrans*) and black bear (*Ursus americanus*) have increased in New Hampshire since the 1980s (unpublished data, NHFG). The influence of winter weather must also be considered since white-tailed deer in New Hampshire are near the northern limit of their range. Severe winter conditions such as deep snow and low temperature can substantially impact population dynamics through mortality and reduced productivity (Verme 1963, 1968, 1977, Lavigne 1999). Lastly, the influence and change in hunter selectivity can affect harvest data. As a population increases and more adult does are available, hunters may become less likely to harvest fawns (Coe et al. 1980), thus reducing the fawn:doe ratio in the harvest. Effective management of New Hampshire's deer population requires that additional and current data be collected to better understand relationships among deer productivity and physical condition, habitat quality, winter severity, and predation. This study was designed to 1) assess the current productivity of the deer herd and compare it to productivity during the 1970s and 1980s, 2) assess the winter nutritional condition of deer, and 3) compare productivity, recruitment, and physical condition of New Hampshire deer to deer populations in nearby jurisdictions.

STUDY AREA

Winter-killed deer for this study were collected throughout the entire state of New Hampshire. The study area was divided into 3 regions based on similarities in deer density, habitat quality, and winter severity. The North region consists of NHFG wildlife management units (WMUs) A, B, C1, C2, D1, D2E, E, F, and G2, the South region consists of WMUs D2W, G1, H1, H2, I1, I2, J1, J2, and K, and the Seacoast region consists of WMUs L and M (Fig. 1).

The North region is predominately forested, including the White Mountain National Forest and many large tracts of commercial timberland. Terrain is hilly to mountainous with elevations ranging from 200-1900 m. The average growing season (number of days between killing frosts) is ~100 days (DeGraaf et al. 1992), and average annual snowfall is 240 cm (95 in; NCDC 2013). The region is dominated by northern hardwoods including sugar (*Acer saccharum*) and red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Red spruce (*Picea rubens*)-balsam fir (*Abies balsamea*) forests tend to dominate both low and high elevations (Sperduto and Kimball 2011). The estimated deer density was 2 deer/km^2 (unpublished data, NHFG).

The South region is hilly and mostly forested with elevations ranging from 90-900 m. The average growing season is 120-150 days (DeGraaf et al. 1992), and average annual snowfall is 180 cm (72 in; NCDC 2013). Northern hardwood forests are common with occasional spruce-fir at higher elevations; white pine (*Pinus strobus*), hemlock (*Tsuga canadensis*), and red oak (*Quercus rubra*) are also dominant at mid-low

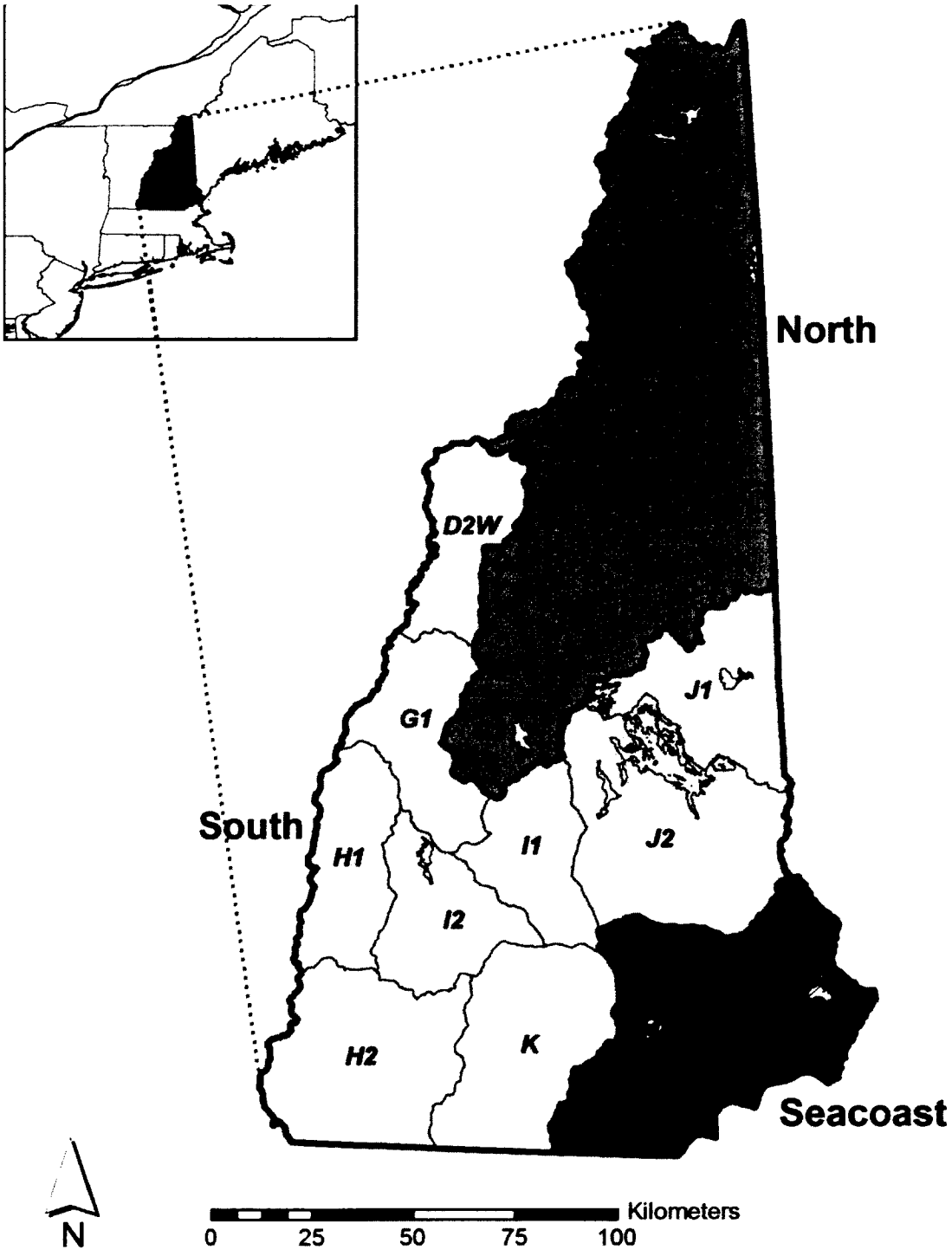

Figure 1. Location of the 3 study regions and New Hampshire Fish and Game Department wildlife management units. Regions were developed based on similarities in deer density, habitat quality, and winter severity.

elevations (Sperduto and Kimball 2011). The estimated deer density was 4 deer/km^2 (unpublished data, NHFG).

The Seacoast region consists of flat to gently rolling terrain with elevations ranging from sea level to ~300 m and relatively substantial human development. Climate in the Seacoast region is moderated by the Atlantic Ocean; the average growing season is ~150 days (DeGraaf et al. 1992), and average annual snowfall is 150 cm (59 in; NCDC 2013). White pine and red oak are dominant, with hemlock, red maple, black birch (*Betula lenta*), and shagbark hickory (*Carya ovata*) also common (Sperduto and Kimball 2011). The estimated deer density was 7 deer/km^2 (unpublished data, NHFG). Possible predators of white-tailed deer in New Hampshire included coyote (*Canis latrans*), black bear (*Ursus americana*), and bobcat (*Lynx rufus*).

CHAPTER I

PRODUCTIVITY OF WHITE-TAILED DEER IN NEW HAMPSHIRE

Introduction

White-tailed deer (*Odocoileus virginianus*) are an important ecological, recreational, and economic resource in New Hampshire, but recently, managers have had difficulty achieving regional population objectives. Reliable estimates of population parameters are necessary to effectively manage deer populations and historically, these parameters have been based on readily available data from legally harvested deer. Although these data are informative and easily obtained, they only provide an index of population health and productivity and are restricted seasonally.

White-tailed deer populations typically exist at or near environmental carrying capacity (McCullough 1999). The relationship between physical condition and density is well established (McCullough 1979), and deer managers often rely on variation in physical parameters such as body weight and antler measurement as indicators of herd health. These physical condition-density relationships hold true over a wide range of densities and habitat conditions, but may be unreliable for low density populations on poor sites or in areas with highly variable environmental conditions (McCullough 1999, Keyser et al. 2005b). The negative correlation between density and productivity is also well established (Cheatum and Severinghaus 1950, Dusek et al. 1989, Verme 1969, Woolf and Harder 1979, Ozoga and Verme 1982); measures of productivity respond to

changes in density more rapidly than physical condition and may be less sensitive to density-independent influences (Keyser et al. 2005a).

Litter size in white-tailed deer varies from 1-3 and is related directly to physical condition of the mother (Verme 1965, 1969, McCullough 1979, Ozoga and Verme 1982). The influence of range condition on litter size is most pronounced in the yearling and fawn age classes, as they allocate energy intake to adequate growth before reproduction. Fawns, if they breed at all, and many yearlings typically conceive a single fetus, whereas mature does under adequate nutritional conditions typically conceive twins (Severinghaus and Cheatum 1956, Verme 1969). Maximum production occurs in prime-aged females (3–7 years old) and probably declines thereafter (Verme and Ullrey 1984). However, there is no evidence of reproductive senescence in older age classes based on pregnancy and fecundity rates (Robinette et al. 1955, Nelson and Mech 1990, DelGiudice et al. 2007); survival of fawns born to older mothers may be lower (Dusek et al. 1989, DelGiudice et al. 2007).

Although younger age classes typically exhibit lower fecundity and pregnancy rates (DelGiudice et al. 2007), they have a significant influence on population growth because they account for a greater proportion of the population than older age classes; this is particularly true in hunted populations. Severinghaus and Cheatum (1956) estimated that yearlings could produce >40% of the annual fawn crop in western New York, and the fawn cohort alone accounted for 30% of annual production in Iowa where >65% of fawns reproduced (Haugen 1975). Pregnancy rates in fawns can range from 0->70%, but are usually minimal in areas with severe winters such as New Hampshire

(Mundinger 1981, Ozoga and Verme 1982, Dusek et al. 1989, Campbell et al. 2005, DelGiudice et al. 2007).

The pregnancy rate in fawns is related to the proportion of individuals that attain puberty before the end of the breeding season, which may occur at 6-7 months of age. Variation in forage quantity or quality and environmental conditions presumably influences the incidence of puberty and the number of individuals that reach critical mass and condition thresholds prior to onset of winter weather (Ransom 1967, Verme and Ozoga 1987, Dusek et al. 1989, Strickland et al. 2008). In northern regions a negative energy balance is realized by early winter, and fawns presumably conserve energy for survival instead of reproduction (Verme and Ullrey 1984).

The New Hampshire Fish and Game Department's (NHFG) current deer management system incorporates reproductive data derived from studies conducted by NHFG in the late 1970s and early 1980s. Deer densities have increased substantially since that time whereas indices of productivity have declined consistently. Biological check stations are run annually by NHFG to collect data for physical condition and productivity indices, including fall lactation rates. Lactation rates and harvest fawn:doe ratio show consistent decline since the 1980s; conversely, yearling antler beam diameter (YABD), a traditional index used to assess population density relative to carrying capacity, has not changed (unpublished data, NHFG).

Possible explanations for this seeming contradiction between declining productivity indices versus stable YABD include predation impacts, unreliable indices, and herd composition. Increased predation on fawns may be occurring and could provide a simple explanation for decline in recruitment to fall. Black bear (*Ursus americanus*),

eastern coyote (*Canis latrans*), and bobcat (*Lynx rufus*) populations have increased in New Hampshire over the last 40 years (unpublished data, NHFG), and many studies indicate that these are substantial predators (particularly coyotes and black bears) of fawns (e.g., Long et al. 1998, Ballard et al. 1999, Patterson et al. 2002, Campbell et al. 2005, Carstensen et al. 2009). Also of concern is that YABD may not provide a sensitive enough index of density relative to carrying capacity and may be influenced by severe winters; direct measurement of productivity (e.g., pregnancy rate, fetal counts) might provide a more sensitive index of declining habitat quality as population density increases (Verme and Ullrey 1984, Keyser et al. 2005a). Recruitment indices from harvested deer may also be unreliable and biased by hunter selectivity. As the population increased and more adult does were available to hunters, some may have become less likely to harvest fawns (Coe et al. 1980) thus reducing the proportion of fawns in the harvest. Finally, a reduction in fawn production could occur from severely skewed sex ratios (as reported by hunters) that impact breeding ecology to the point where substantial numbers of does are not bred, thereby either reducing pregnancy rates or shifting the breeding cycle into the second estrus in December.

The difficult, yet important task of interpreting and predicting the status of New Hampshire's deer population requires that additional and current biological data be collected to better assess the relative condition and productivity of the population. This study assessed the current reproductive attributes of New Hampshire's deer herd through the direct measurement of ovulation rates, pregnancy rates, and fetal counts from winter mortalities, and compared these data with past productivity data.

Methods

Sample Collection

Biological samples were collected from winter deer mortalities from late December through mid-May in 2010-2011, 2011-2012, and 2012-2013; this time frame coincides with the gestation period for white-tailed deer in New Hampshire. Necessary biological samples or whole carcasses were collected by NHFG or University personnel and frozen until later processing. Each deer was identified by a unique identification number, kill date, and location. Biological samples collected from each deer included a central incisor and the reproductive tract including ovaries, uterus, and any fetus.

The study area was divided into three regions based on similarities in deer density, habitat quality, and winter severity. The North region consists of NHFG wildlife management units (WMUs) A, B, C1, C2, D1, D2E, E, F, and G2, the South region consists of WMUs D2W, G1, H1, H2, I1, I2, J1, J2, and K, and the Seacoast region consists of WMUs L and M (Fig. 1).

Deer were aged based on tooth replacement and wear techniques (Severinghaus 1949) and cementum annuli analysis from an extracted central incisor (Gilbert 1966, Low and Cowan 1963); cementum analysis was performed by Matson's Laboratory (Milltown, Montana). Tooth replacement and wear was used to distinguish fawns from deer >1 year old and to age deer not aged by cementum analysis. For most analyses deer were grouped into 3 age classes; fawn (0.5-1 year old), yearling (1.5-2 years old), and adult (>2.5 years old).

Ovulation Rate

Ovulation rate was measured via counts of corpora lutea (CL) of pregnancy from complete sets of ovaries (Cheatum 1949a). Once detached from the uterus, ovaries were fixed in ethanol and stored in sealed plastic containers. After ≥48 h, ovaries were sectioned with a razorblade to count CL. The total number of CL in each pair of ovaries was recorded and fertility (the proportion of does with ≥1 CL) and ovulation rate (number of CL per doe with CL) were determined for each age class. Analysis of variance (ANOVA) was used to detect differences in ovulation rate between age classes, regions, and sample years; pairwise comparisons were made with Tukey's test. Fisher's exact test was used to test for differences in fertility between age classes, regions, and sample years.

Fecundity and Pregnancy Rates

Pregnancy was determined by the presence of ≥1 embryo or fetus or examination of the uterus. When fetuses were ejected from roadkilled deer or scavenged, pregnancy could be determined by the presence of cotyledons or enlarged caruncles in the uterus, but litter size was unknown. For deer killed prior to implantation of embryos, pregnancy was determined by the presence of CL of pregnancy in ovaries and visible enlargement of the uterus. If pregnancy status was inconclusive, deer were excluded from analyses. Pregnancy rate was calculated as the proportion of does in each age class determined to be pregnant.

Visible embryos and fetuses were removed from the uterus, and the interior of the uterus completely examined for recently implanted embryos, resorbing fetuses, or any evidence thereof. The number of embryos or fetuses, including dead or non-viable

fetuses, was recorded and each fetus was sexed if possible. Does with unknown litter size were excluded and data were pooled by age class to determine age-specific fecundity (fetuses per pregnant doe) and birth rates (viable fetuses per doe). Differences in fecundity and birth rate between age classes, regions, and sample years were detected using ANOVA; pairwise comparisons were made with Tukey's test. Fisher's exact test was used to test for differences in pregnancy rate, distribution of litter sizes, and fetal sex ratios between age classes, regions, and sample years.

Breeding and Parturition Dates

It is possible to estimate fetal age, and consequently breeding and parturition dates, from physical measurements of fetuses (Armstrong 1950, Short 1970, Hamilton et al. 1985). After being excised from the uterus, excess fluid and extraneous membranes were removed and fetuses were weighed to the nearest gram. The forehead to rump length (crown-rump for embryos) was measured (nearest mm) on each fetus using calipers with the fetus lying in a natural position. Age in days was estimated using crown/forehead-rump length and predictive equations developed by Hamilton et al. (1985). Although this equation was developed for the smaller, southeastern subspecies of white-tailed deer, predicted age is within ±5 days of that estimated with methods of Cheatum and Morton (1946; New York deer) and from a much larger sample size. These studies are based on samples obtained from captive deer fed high quality diets *ad libitum*; therefore, it is reasonable to believe that fetal growth in nutritionally restricted wild northern deer may be lower (Verme 1963), and therefore more closely approximate the observations of Hamilton et al. (1985). Mean length was used to estimate age of twin and triplet fetuses; age of triplets was estimated using the equation for twins as no equation

was provided for triplets. Breeding date was determined by subtracting age in days from the kill date. Parturition date was calculated by subtracting age in days from 200 (mean gestation period; Cheatum and Morton 1946), then adding the remainder to the kill date. Due to the skewed distribution of breeding date data, the Kruskal-Wallis test was used to detect differences in breeding date among age classes, within age classes between years, and among litter sizes within age classes; pairwise comparisons were made using Wilcoxon rank sum tests.

Comparison to Historic Productivity

Current productivity data were compared to similar productivity data collected by NHFG during 1972 and 1975-1987; historic data were divided into 2 time periods (1972-1980 and 1981-1987) based on differences in productivity, winter severity (WSI), and deer harvests during that time. The WSI is the sum of the number of days with low temperature $\leq$-18° C (0° F) and the number of days with snow depth $\geq$46 cm (18 in). The statewide median WSI during 1972-1980 was 62; the median WSI was 39 from 1981-1987, with only one year >62. Additionally, current ovulation data were compared to ovulation data collected by NHFG during 1951-1954 and 1981-1984. An ANOVA was used to detect differences in fertility, ovulation rate, pregnancy, fecundity, and birth rate among time periods and age classes; pairwise comparisons were made with Tukey's test. All statistical analyses were performed in JMP 10 (SAS Institute Inc. 2007); significance level was set *a priori* at $\alpha = 0.05$ for all tests.

Potential recruitment was estimated for each time period based on age-specific birth rates and the age distribution of the population. Age distribution was based on the proportion of harvested deer examined by biologists that were 1.5, 2.5, and $\geq$3.5 years

old; these deer would have been fawns, yearlings, and adults (≥2.5 year old) when they bred. Therefore, potential recruitment was the maximum number of fawns per doe at the beginning of the hunting season, assuming 100% survival of fawns whose mother survives and 0% survival if not. Potential recruitment was compared to observed recruitment (harvest fawn:doe ratio based on registration station data) as an index of summer fawn mortality.

Results

Reproductive tracts were collected from 249 female deer; including 65 (26%) fawns, 20 (8%) yearlings, 155 (62%) adults, and 9 (4%) deer of unknown age (Table 1.1). More deer were collected in 2010-2011 (n = 127) than in 2011-2012 (n = 51) or 2012-2013 (n = 71); distribution among age classes was similar between years. Mean age of 137 deer ≥1 year old based on cementum annuli analysis was 6.3 years, (range = 1-17); 30% were ≥9 years old (Fig. 1.1). Deer were collected from 113 towns located throughout the state (Fig 1.2); 24 (10%) were from the town of Pittsburg in far northern New Hampshire. Overall, 88 deer were collected from the North region, 120 from the South, and 37 from the Seacoast. Sampling density was relatively even among regions (range = 1.0-1.6 deer/100 km^2), but was not related to estimated regional deer densities. Samples were collected from 219 (88%) roadkills, 14 (6%) nuisance/damage permit kills, 5 (2%) coyote kills, 2 (1%) bobcat kills, 2 (1%) illegal kills, 2 (1%) euthanized by NHFG, 1 (<1%) hit by a train, and 4 (2%) unknown.

Table 1.1. Age class distribution of female white-tailed deer collected during December–May, 2010–2013. Age was determined by cementum annuli analysis or tooth replacement and wear.

	2011	**2012**	**2013**	**Total**
Fawn	28 (22%)	17 (33%)	20 (28%)	65 (26%)
Yearling	12 (9%)	5 (10%)	3 (4%)	20 (8%)
Adult	82 (65%)	28 (55%)	45 (63%)	155 (62%)
Unknown	5 (4%)	1 (2%)	3 (4%)	9 (4%)
Total	127	51	71	249

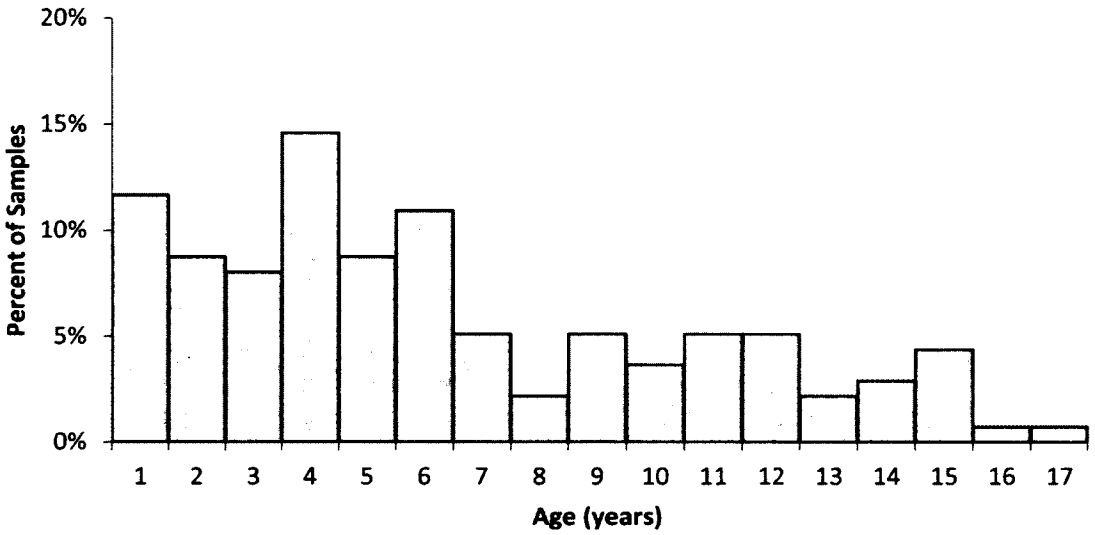

Figure 1.1. Age distribution of 137 female white-tailed deer (≥1 year old) killed during January–May 2011–2013, in New Hampshire and aged by cementum annuli analysis.

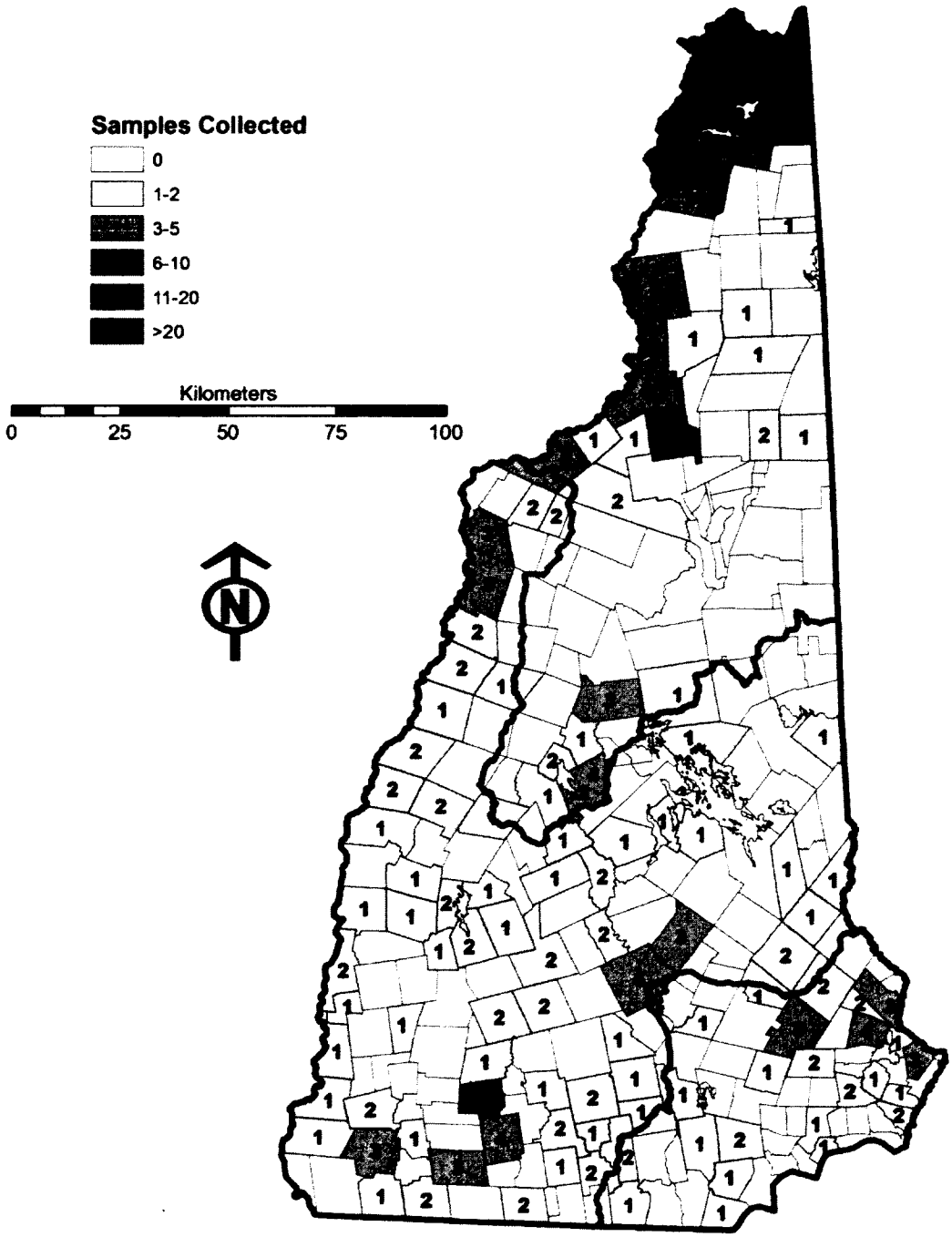

Figure 1.2. Collection locations by town for 242 deer sampled during December–May 2010–2013. Samples were evenly distributed in the South and Seacoast, but concentrated near wintering areas and supplemental feeding sites in the North.

Ovulation

Complete pairs of ovaries were collected from 55 fawns; 4 (7%) produced a total of 5 CL. Complete pairs were collected from 13 yearlings and 115 adults; all yearlings and 112 (97%) adults contained CL (Table 1.2). Fertility of adults and yearlings was not different ($P = 0.51$), but both were greater than fawns ($P < 0.001$ in both cases). The adult ovulation rate of 2.13 CL per pregnant doe was greater than that of yearlings (1.62; $P = 0.007$) and fawns (1.25; $P = 0.005$); yearlings and fawns were not different ($P = 0.32$; Table 1.3). In the North, ovulation rates of adults and yearlings were similar (2.14 and 2.00, respectively; $P = 0.98$), and the single pregnant fawn had 2 CL. In the South, adult ovulation rate (2.19) was greater than in yearlings (1.33; $P < 0.001$) and the single pregnant fawn had 1 CL. The adult ovulation rate in the Seacoast was 1.92 and both pregnant fawns and the single yearling each had a single CL. There were no differences ($P < 0.05$) in fertility or ovulation rate among regions, within regions among years, or among years for pooled data in any age class.

Pregnancy and Fecundity

Sufficiently intact uteri were collected from 60 fawns of which 5 (8%) were pregnant. Adult and yearling pregnancy rates were not different (97% and 100%, respectively; $P = 0.42$), but both were greater than fawns ($P < 0.001$; Table 1.4). There were no differences in pregnancy rate among regions, within regions among years, or among years for pooled data for any age class.

Only 3 of the 5 pregnant fawns contained macroscopic embryos. Adult fecundity (1.95 fetuses per pregnant doe) was 95% greater than fawns (1.00; $P = 0.022$) and 13% greater than yearlings (1.72); adults and yearlings were not different ($P = 0.284$), albeit

Table 1.2. Fertility rate of white-tailed deer by sample region in New Hampshire, 2011-2013. Fertility rate is the proportion of does collected during December-May with ≥1 CL in the ovaries. Values are mean±SE; sample sizes are in parentheses.

	Region	2011	2012	2013	Total
Fawn	North	0.00±0.00 (7)	0.00±0.00 (3)	0.33±0.27 (3)	0.08±0.07 (13)
	South	0.08±0.07 (13)	0.00±0.00 (9)	0.00±0.00 (6)	0.04±0.04 (28)
	Seacoast	0.00±0.00 (4)	0.50±0.35 (2)	0.14±0.13 (7)	0.15±0.10 (13)
	Statewide[1]	0.04±0.04 (24)	0.07±0.06 (15)	0.13±0.08 (16)	0.07±0.04 (55)
Yearling	North	1.00±0.00 (3)	1.00±0.00 (1)	1.00±0.00 (2)	1.00±0.00 (6)
	South	1.00±0.00 (3)	1.00±0.00 (3)	-	1.00±0.00 (6)
	Seacoast	-	1.00±0.00 (1)	-	1.00±0.00 (1)
	Statewide	1.00±0.00 (6)	1.00±0.00 (5)	1.00±0.00 (2)	1.00±0.00 (13)
Adult	North	0.94±0.06 (17)	0.90±0.09 (10)	1.00±0.00 (19)	0.96±0.03 (46)
	South	1.00±0.00 (38)	1.00±0.00 (7)	1.00±0.00 (9)	1.00±0.00 (54)
	Seacoast	0.90±0.09 (10)	1.00±0.00 (3)	1.00±0.00 (1)	0.93±0.07 (14)
	Statewide[1]	0.97±0.02 (66)	0.95±0.05 (20)	1.00±0.00 (29)	0.97±0.01 (115)

[1]Region was not known for some individuals included in statewide totals

Table 1.3. Ovulation rate of white-tailed deer by sample region in New Hampshire, 2011-2013. Ovulation rate is the number of CL per doe with ≥1 CL, based on examination of does collected during December-May. Values are mean±SE; sample sizes are in parentheses.

	Region	2011	2012	2013	Total
Fawn	North	-	-	2.00±0.00 (1)	2.00±0.00 (1)
	South	1.00±0.00 (1)	-	-	1.00±0.00 (1)
	Seacoast	-	1.00±0.00 (1)	1.00±0.00 (1)	1.00±0.00 (2)
	Statewide	1.00±0.00 (1)	1.00±0.00 (1)	1.50±0.50 (2)	1.25±0.25 (4)
Yearling	North	2.00±0.00 (3)	3.00±0.00 (1)	1.50±0.50 (2)	2.00±0.26 (6)
	South	1.33±0.33 (3)	1.33±0.33 (3)	-	1.33±0.21 (6)
	Seacoast	-	1.00±0.00 (1)	-	1.00±0.00 (1)
	Statewide	1.67±0.21 (6)	1.60±0.40 (5)	1.50±0.50 (2)	1.62±0.18 (13)
Adult	North	2.13±0.13 (16)	2.11±0.20 (9)	2.16±0.14 (19)	2.14±0.08 (44)
	South	2.24±0.09 (38)	2.00±0.20 (7)	2.11±0.11 (9)	2.19±0.07 (54)
	Seacoast	2.00±0.17 (9)	2.00±0.00 (3)	1.00±0.00 (1)	1.92±0.14 (13)
	Statewide[1]	2.17±0.07 (64)	2.05±0.12 (19)	2.10±0.10 (29)	2.13±0.05 (112)

[1]Region was not known for some individuals included in statewide totals

Table 1.4. Pregnancy rates of white-tailed deer by sample region in New Hampshire, 2011-2013. Pregnancy was determined by examination of reproductive tracts collected from incidental mortalities during December-May. Values are mean±SE; sample sizes are in parentheses.

	Region	2011	2012	2013	Total
Fawn	North	0.00±0.00 (8)	0.00±0.00 (4)	0.25±0.22 (4)	0.06±0.06 (16)
	South	0.07±0.07 (14)	0.00±0.00 (9)	0.00±0.00 (6)	0.03±0.04 (23)
	Seacoast	0.00±0.00 (4)	0.50±0.35 (2)	0.25±0.15 (8)	0.21±0.11 (14)
	Statewide[1]	0.04±0.04 (26)	0.06±0.06 (16)	0.17±0.09 (18)	0.08±0.04 (60)
Yearling	North	1.00±0.00 (5)	1.00±0.00 (1)	1.00±0.00 (2)	1.00±0.00 (8)
	South	1.00±0.00 (7)	1.00±0.00 (2)	-	1.00±0.00 (9)
	Seacoast	-	1.00±0.00 (1)	1.00±0.00 (1)	1.00±0.00 (2)
	Statewide	1.00±0.00 (12)	1.00±0.00 (4)	1.00±0.00 (7)	1.00±0.00 (19)
Adult	North	0.96±0.04 (23)	0.83±0.11 (12)	1.00±0.00 (21)	0.96±0.03 (55)
	South	1.00±0.00 (44)	1.00±0.00 (10)	1.00±0.00 (18)	1.00±0.00 (72)
	Seacoast	0.91±0.09 (11)	1.00±0.00 (5)	1.00±0.00 (3)	0.95±0.05 (19)
	Statewide[1]	0.97±0.02 (79)	0.93±0.05 (27)	1.00±0.00 (42)	0.97±0.01 (148)

[1]Region was not known for some individuals included in statewide totals

yearling sample size was limited (Table 1.5). There were no differences in fecundity among regions for any age class, but yearling fecundity was generally higher in the North (1.86) than the South (1.67) or Seacoast (1.50; Table 1.5). There were no differences in fecundity among years or within regions among years for any age class; however, adult fecundity in the South was 20% lower in 2012 (1.60) than 2011 (2.02) or 2013 (2.00).

Twelve fetuses (4%; 7 in 2011, 2 in 2012, and 3 in 2013) from 7 adult does were being resorbed and are not included in the birth rate; 2 additional does had completely resorbed their fetuses. Birth rates of adults (1.80 viable fetuses per doe) and yearlings (1.72) were not different ($P = 0.50$) but both were greater than the fawn birth rate (0.05; $P < 0.001$); this pattern was similar across all regions. There were no differences in birth rate among regions, within regions among years, or among years for pooled data for any age class; however, similar to fecundity, adult birth rate in the South was >26% lower in 2012 (1.40) than 2011 (1.93) or 2013 (1.88). A similar pattern was observed in the North, where the adult birth rate decreased 14% from 2011 to 2012 and then increased 22% from 2012 to 2013 (Table 1.6).

All pregnant fawns carried single fetuses, and litter size ranged from 1-3 for deer >1 year old. Overall, yearlings carried 33% singletons, 61% twins, and 6% triplets, and adults carried 20% singletons, 66% twins, and 14% triplets. The single yearling carrying triplets was collected in the North region; no triplets were collected from any age class in the Seacoast. There were no differences in distribution of litter sizes among regions, within regions among years, or among years for pooled data.

Yearlings produced 59% female fetuses (11M:16F) and adults 52% (113M:121F); the only fetus from a fawn that could be sexed was female. Fetal sex ratios were not

Table 1.5. Fecundity (fetuses per pregnant doe) of white-tailed deer by sample region in New Hampshire, 2011-2013. Values are mean±SE; sample sizes are in parentheses.

	Region	2011	2012	2013	Total
Fawn	North	-	-	1.00±0.00 (1)	1.00±0.00 (1)
	South	1.00±0.00 (1)	-	-	1.00±0.00 (1)
	Seacoast	-	-	1.00±0.00 (1)	1.00±0.00 (1)
	Statewide	1.00±0.00 (1)	-	1.00±0.00 (2)	1.00±0.00 (3)
Yearling	North	1.80±0.20 (5)	3.00±0.00 (1)	1.00±0.00 (1)	1.86±0.26 (7)
	South	1.71±0.18 (7)	1.50±0.50 (2)	-	1.67±0.17 (9)
	Seacoast	-	1.00±0.00 (1)	2.00±0.00 (1)	1.50±0.50 (2)
	Statewide	1.75±0.13 (12)	1.75±0.48 (4)	1.50±0.50 (2)	1.72±0.14 (18)
Adult	North	2.00±0.13 (19)	2.00±0.31 (7)	1.95±0.15 (20)	1.98±0.10 (46)
	South	2.02±0.10 (41)	1.60±0.16 (10)	2.00±0.09 (16)	1.96±0.07 (67)
	Seacoast	1.89±0.11 (9)	2.00±0.00 (5)	1.33±0.33 (3)	1.82±0.10 (17)
	Statewide[1]	2.00±0.07 (70)	1.82±0.13 (22)	1.92±0.09 (39)	1.95±0.05 (131)

[1]Region was not known for some individuals included in statewide totals

Table 1.6. Birth Rates (viable fetuses per doe) of white-tailed deer by sample regions in New Hampshire, 2011-2013. Dead or resorbing fetuses are not included in the birth rate. Values are mean±SE; sample sizes are in parentheses.

	Region	2011	2012	2013	Total
Fawn	North	0.00±0.00 (8)	0.00±0.00 (4)	0.25±0.25 (4)	0.06±0.00 (16)
	South	0.07±0.07 (14)	0.00±0.00 (9)	0.00±0.00 (6)	0.03±0.00 (29)
	Seacoast	0.00±0.00 (4)	0.00±0.00 (1)	0.14±0.14 (7)	0.08±0.00 (12)
	Statewide[1]	0.04±0.04 (26)	0.00±0.00 (15)	0.12±0.08 (17)	0.05±0.03 (58)
Yearling	North	1.80±0.20 (5)	3.00±0.00 (1)	1.00±0.00 (1)	1.86±0.26 (7)
	South	1.71±0.18 (7)	1.50±0.50 (2)	-	1.67±0.17 (9)
	Seacoast	- - -	1.00±0.00 (1)	2.00±0.00 (1)	1.50±0.50 (2)
	Statewide	1.75±0.13 (12)	1.75±0.48 (4)	1.50±0.50 (2)	1.72±0.14 (18)
Adult	North	1.75±0.18 (20)	1.56±0.38 (9)	1.90±0.16 (20)	1.78±0.12 (49)
	South	1.93±0.12 (41)	1.40±0.22 (10)	1.88±0.15 (16)	1.84±0.09 (67)
	Seacoast	1.70±0.21 (10)	2.00±0.00 (5)	1.33±0.33 (3)	1.72±0.14 (18)
	Statewide[1]	1.85±0.09 (72)	1.58±0.17 (24)	1.85±0.11 (39)	1.80±0.06 (135)

[1]Region was not known for some individuals included in statewide totals

different among age classes, regions, or within regions among years. Adult fetal sex ratio was not different among years (47-54% female), but the yearling fetal sex ratio declined from 74% female in 2011 to 0% female in 2012 (P = 0.028).

Breeding and Parturition

Breeding date could only be estimated for 2 pregnant fawns which conceived on 16 December and 20 December with estimated parturition dates of 4 and 8 July, respectively. For 19 yearlings, the median breeding and parturition dates were 26 November and 14 June, respectively; breeding dates ranged from 3 November to 22 December, with 37% from 18-26 November (Fig. 1.3). The median breeding and parturition dates for 129 adult does were 20 November and 8 June, respectively. Breeding dates ranged from 4 November to 8 January, with 59% from 13-26 November (Fig. 1.3). Adults bred earlier than fawns ($P = 0.021$); yearlings were not different from adults ($P = 0.191$) or fawns ($P = 0.105$), albeit sample sizes were limited. There was no difference in breeding chronology among years, regions, or within regions among years; however, yearlings in the North bred 14 days later (6 December) than yearlings in the South (22 November; $P = 0.080$). Adult deer carrying a single fetus bred later (27 November) than deer carrying twins (19 November; $P = 0.027$) or triplets (18 November; $P = 0.008$). Adults that bred on or before 20 November were more fecund (2.14 fetuses per pregnant doe) than deer that bred later (1.77; $P < 0.001$).

Historical Comparison

There were no differences in ovulation rate among time periods in any age class. Fertility rates of adults and yearlings were lower in 1951-1954 (0.75, 0.76, respectively) than in 1981-1984 (0.91, 1.00; $P < 0.02$) or 2011-2013(0.97, 1.00; $P < 0.005$); there were

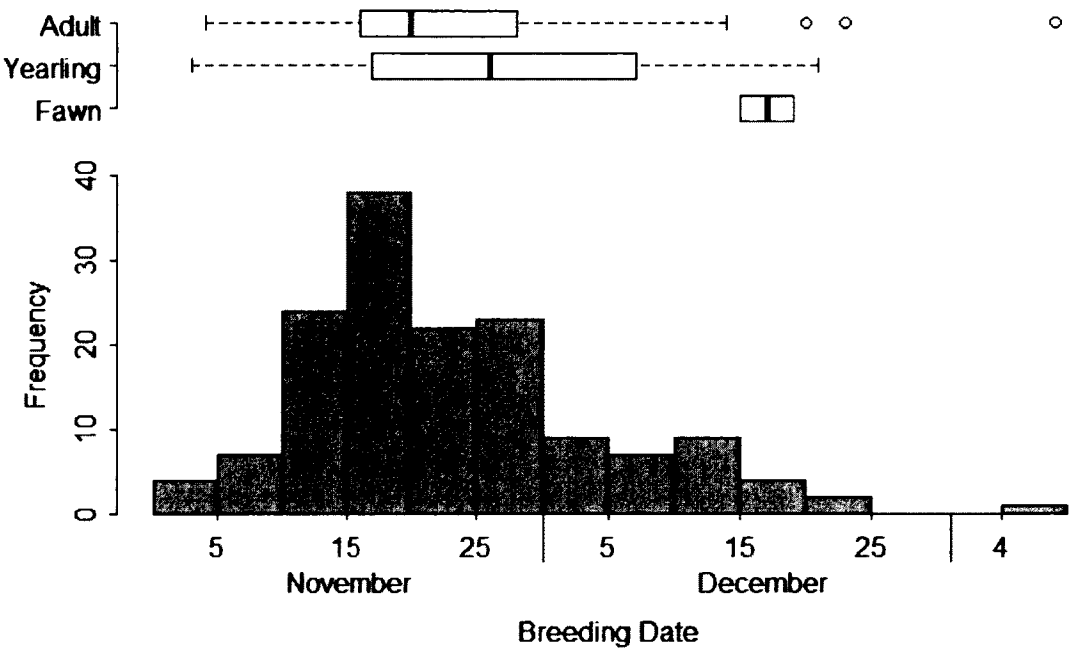

Figure 1.3. Estimated breeding dates of white-tailed deer in New Hampshire during 2010-2012 (n = 150) based on fetal measurements and predictive equations of Hamilton et al. (1985). Boxplots show age-specific median breeding dates (dark line), middle 50% of data (box), approximate 95% confidence intervals ("whiskers"), and outliers (circles).

no differences (P>0.05) between 1981-1984 and 2011-2013 (Table 1.7). There were no differences among time periods in the fertility rate of fawns, although it declined 42% from 1981-1984 (0.19) to 2011-2013 (0.08; P = 0.50).

There was no change in pregnancy rate, fecundity, or birth rate in the adult age class among time periods (P >0.05; Table 1.8). Yearling fecundity was not different between time periods (P = 0.94), but yearling pregnancy rate was lower in 1972-1980 than 1981-1987 (P <0.001) and 2011-2012 (P <0.001); there was no difference between 1981-1987 and 2011-2012 (P = 0.87). The increase in the pregnancy rate resulted in a corresponding increase in the birth rate from 1972-1980 to 1981-1987 (P = 0.002) and 2011-2012 (P = 0.006). Fawn pregnancy rate was greater during 1981-1987 than in 1972-1980 (P = 0.006) and 2011-2012 (P = 0.048). This resulted in a similar increase in fawn birth rate during 1981-1987 compared to 1972-1980 (P = 0.001) and 2011-2012 (P = 0.007). There was no change in fawn fecundity among time periods (P = 0.43; Table 1.8).

Potential recruitment increased 14% from 1972-1980 (1.03 fawns per doe) to 1981-1987 (1.17), and 18% from 1981-1987 to 2011-2013 (1.39; Fig. 1.4). Conversely, observed recruitment declined 37% from 1981-1987 (0.81 fawns per doe) to 2011-2013 (0.51). Assuming that the fawn:doe ratio in the harvest is representative of the population, summer fawn mortality increased from 31% in 1981-1987 to 65% in 2011-2013.

Table 1.7. Age-specific fertility and ovulation rate of white-tailed deer in New Hampshire during three time periods. Values are mean±SE.

	Period	Fertility	Ovulation Rate
Fawn	1951-1954	0.37±0.13	1.21±0.08
	1981-1984	0.19±0.13	1.18±0.11
	2011-2013	0.08±0.15	1.17±0.11
Yearling	1951-1954	0.77±0.01	1.63±0.23
	1981-1984	1.00±0.01	1.92±0.23
	2011-2013	1.00±0.01	1.59±0.27
Adult	1951-1954	0.82±0.04	2.02±0.09
	1981-1984	0.91±0.04	2.06±0.09
	2011-2013	0.97±0.05	2.11±0.10

Table 1.8. Age-specific pregnancy, fecundity, and birth rates of white-tailed deer in New Hampshire during three time periods. Values are mean±SE.

	Period	Pregnancy	Fecundity	Birth Rate
Fawn	1972-1980	0.07±0.04	1.00±0.05	0.07±0.02
	1981-1987	0.28±0.04	1.07±0.04	0.30±0.04
	2011-2013	0.09±0.06	1.00±0.07	0.02±0.01
Yearling	1972-1980	0.73±0.03	1.64±0.08	1.17±0.07
	1981-1987	0.97±0.03	1.68±0.08	1.63±0.07
	2011-2013	1.00±0.05	1.67±0.13	1.67±0.11
Adult	1972-1980	0.89±0.02	1.80±0.05	1.59±0.06
	1981-1987	0.92±0.02	1.80±0.05	1.65±0.06
	2011-2013	0.97±0.03	1.91±0.07	1.76±0.09

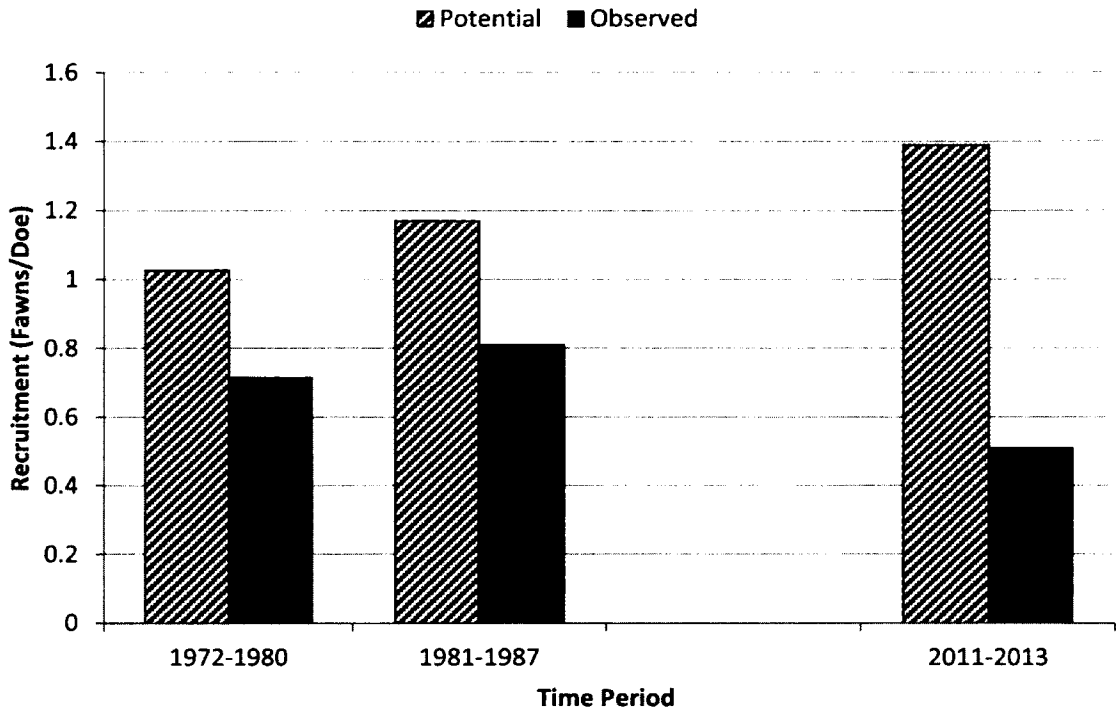

Figure 1.4. Potential and observed recruitment of white-tailed deer fawns in New Hampshire during three time periods. Potential recruitment is calculated from age-specific birth rates and the proportion of those age classes in the following harvest and assumes 100% fawn survival. Observed recruitment is the ratio of fawns to does >1 year old in the harvest.

Discussion

Fecundity and pregnancy rates of adult and yearling deer in New Hampshire were relatively high compared to other northern populations (i.e., areas with severe winters) (Ontario, Mansell 1974; Montana, Dusek et al. 1989; Minnesota, DelGiudice et al. 2007), and generally are exceeded only by populations in areas with extensive agriculture (e.g., Ransom 1967, Haugen 1975). These data clearly indicate a population in excellent health with high reproductive potential. No age-related differences in pregnancy or fecundity were observed for deer 1-17 years old; however, larger sample size probably would have indicated lower fecundity in yearlings than older deer as seen in other studies (e.g., Severinghaus and Cheatum 1956, Ransom 1967, Roseberry and Klimstra 1970, Mansell 1974, DelGiudice et al. 2007). There was no clear evidence of reproductive senescence, although the 2 oldest deer (16 and 17 years) carried single fetuses. In Minnesota, DelGiudice et al. (2007) noted a similar lack of apparent senescence up to 15 years old (the oldest in their study), but suggested that senescence may manifest through reduced birth weight and neonatal survival rather than reduced fertility and fecundity.

The adult ovulation rate (2.13) was greater than yearlings (1.62; Table 1.3), but both are relatively high for those age classes (Roseberry and Klimstra 1970, Haugen 1975, Woolf and Harder 1979, Dusek et al. 1989). The adult fertilization rate (the proportion of ova which result in an embryo) was 93% whereas it was 100% for yearlings. These values are typical of most deer populations and appear to be related to normal variation in reproductive success rather than physical condition, as the more fecund and presumably better conditioned age classes often have the lowest rates

(Ransom 1967, Roseberry and Klimstra 1970, Jacobson et al. 1979, Woolf and Harder 1979, Dusek et al. 1989).

The low pregnancy rate of fawns (8%; Table 1.4) was typical of most northern populations (e.g., New York, Morton and Cheatum 1946; Ontario, Mansell 1974; Montana, Mundinger 1981; Minnesota, Fuller 1990, DelGiudice et al. 2007). Onset of puberty in fawns is determined by complex interrelationships of several factors including body weight and composition, age, heredity, and environmental conditions (Budde 1983, Verme and Ullrey 1984, Verme and Ozoga 1987). In northern regions a negative energy balance is realized by early winter, and fawns presumably conserve energy for survival instead of reproduction (Verme and Ullrey 1984). Variation in forage quantity or quality and environmental conditions presumably influences the incidence of puberty and the number of individuals that reach critical mass and condition thresholds prior to onset of winter weather (Ransom 1967, Verme and Ozoga 1987, Dusek et al. 1989 Strickland et al. 2008). Additionally, winter malnutrition and body condition of females can directly influence birth characteristics of neonates (Verme 1963, 1965, 1969, 1977, Verme and Ozoga 1981), and nutritionally deprived does may allocate less energy to lactation resulting in reduced growth of fawns (Therrien et al. 2008). Three of the 5 pregnant fawns examined in this study were collected in 2013 following the exceptionally mild winter of 2011-2012. The 2011-2012 winter severity index (WSI) of 13 was the lowest since NHFG began calculating WSI in 1965; median statewide WSI was 35, ranging from 13-101 in 1980-2013.

No differences were detected among years in any of the productivity metrics for any age class; however, sample sizes were limited in 2012 and 2013. Mild conditions in

winter 2011-2012 afforded deer near continuous mobility, broad access to natural foods, and less reliance, restriction, and use of traditional wintering areas and supplementary feeding sites common in northern New Hampshire. These conditions resulted in low sample size (n = 51) compared to winter 2010-2011 (n = 127). Winter 2012-2013 was also relatively mild (WSI = 16) and sample size was again relatively low (n = 71).

There is some evidence that previous winter conditions affect productivity, suggesting incomplete recovery in summer-fall (Mech et al. 1987, Garroway and Broders 2005). The 15% decrease in birth rate from 2011-2012 (Table 1.6), although not statistically significant, was likely related to the severe winter of 2010-2011 (WSI = 61). Similarly, the increase in most productivity measures in 2013 following the exceptionally mild winter of 2011-2012 may also indicate some influence of winter severity. The decline from 2011-2012 was most pronounced in the South, where birth rate declined 20% (Table 1.6); although winter 2010-2011 was more severe in the North (WSI = 74), it was only 12% above the long-term regional average while the South (WSI = 50) was 47% above average. It is also possible that an exceptional mast crop of American beech (*Fagus grandifolia*) in 2011 may have masked effects of the severe winter of 2010-2011 in the North. Adult birth rate did decline 14% in the North from 2011-2012, but adult ovulation rate was unchanged while it declined 12% in the South (Table 1.3). Beech is more abundant in the North while northern red oak (*Quercus rubra*) is the predominant mast producing tree in the South and Seacoast; 2011 was a poor-moderate oak mast year (unpublished data, NHFG). Additionally, although most deer in New Hampshire probably have access to supplemental feed during winter (Ross 2003), feeding is more prevalent in the North. Supplemental feeding can have positive influence on the energy

balance of deer during winter (Tarr and Pekins 2002), thus reducing the effects of severe winter conditions.

Differences in productivity among regions might be expected given differences in deer density, habitat quality, and winter severity, but no clear differences were observed. It is possible that differences in density masked the influence of habitat quality and winter severity. Deer in the North arguably exist in lower quality habitat and are exposed to more severe winter conditions than deer in the South or Seacoast, but population density was also less than half that of the other regions. Widespread supplemental feeding during winter, particularly in the North, may also reduce the effect of regional differences in winter severity.

Although small sample sizes limited statistical comparisons to the Seacoast, slightly lower fecundity and the absence of triplet litters suggest that productivity may be lower in this region (Table 1.5). Deer densities were highest in the Seacoast and the lack of triplet litters could be density related; however, all productivity metrics were still relatively high. Mean age of cementum aged deer from the Seacoast (4.1 years) was younger than deer from the South (6.7) or North (6.7); a greater proportion of younger deer (along with small sample size) could account for the lack of triplet litters. Additionally, the sample from the Seacoast included fewer old deer (10% >9 years old) compared to the other regions (both >30%). The younger population age structure in the Seacoast probably reflects the higher antlerless harvest rates (longer season, additional tags) intended to stabilize or reduce the regional density.

Overall, the low proportion of deer 1-3 years old in the sample (25%) compared to 30% ≥9 years old suggests a bias toward older deer (Figure 1.1). This was less

pronounced in 2011-2012 (17% ≥9 years old) compared to 2010-2011 (34%), suggesting severe winter conditions in 2010-2011 disproportionately increased susceptibility of old deer to motor vehicle collisions. This is consistent with the suggestion of O'Gara and Harris (1988) that roadkills may be biased toward poorly conditioned individuals, as these deer may travel along plowed roadways and may be less willing or able to get out of the road when snow is deep. Interestingly, the 2010-2011 sample had a lower proportion of fawns (22%) than the 2011-12 sample (35%), indicating that despite being the most affected age class, severe winter conditions did not disproportionately increase susceptibility of fawns to vehicular collisions. The fawn:doe ratios in the 2011-2012 and 2012-2013 samples (0.52:1 and 0.42:1, respectively; Table 1.1) were similar to the 2011 and 2012 harvest fawn:doe ratios (0.55:1 and 0.47:1, respectively; unpublished data, NHFG), suggesting a representative sample of fawns was collected in those years.

Prenatal fetal mortality has been reported in several studies of white-tailed deer productivity (e.g., Ransom 1967, Mansell and Cringan 1968, Roseberry and Klimstra 1970). It is assumed to result from nutritional constraints of winter, but the impact of this phenomenon is generally minimal (Verme and Ullrey 1984). At least 4% of fetuses examined in this study were being resorbed, which is similar to the rate observed by Roseberry and Klimstra (1970) in southern Illinois, although all of their deer were collected in January and they estimated ~10% total prenatal mortality. Of the 9 deer that were resorbing fetuses, 6 were ≥8 years old of which 4 had marrow fat content ≤50%. The remaining 3 deer were 1, 2, and 6 years old and appeared to be in relatively good condition. Although poor nutritional condition was certainly a factor for some of these deer, it is not apparent what caused the fetal mortality in others.

Breeding Chronology

Onset of breeding in white-tailed deer is ultimately triggered by photoperiod and temperature (Severinghaus and Cheatum 1956, Verme and Ullrey 1984), and does will continue to ovulate until they conceive or winter weather becomes restrictive (Cheatum 1949a, Mansell 1971, 1974, Plotka et al. 1977, Verme and Ullrey 1984).The breeding period in New Hampshire extended from early November through December; 69% bred from 11-30 November (Fig. 1.3). The concise breeding period and mid-to-late November peak was consistent with other northern deer populations (Cheatum and Morton 1946, Severinghaus and Cheatum 1956, Verme 1969, Mansell 1974, Harder and Moorhead 1980), and nearly identical to the breeding period observed during 1951-1954 in New Hampshire (Siegler 1968). Timing and duration of the breeding period was consistent from year to year. Peak breeding was less-pronounced in 2011 and 2012, but this was probably due to smaller sample sizes in those years. In exploited populations with male-biased harvest there may be an insufficient number of bucks to ensure that all does are bred during their first estrus resulting in a prolonged breeding season and later conception dates (Jacobson 1992, DeYoung and Miller 2011). This was not the case in New Hampshire, as there was a single, obvious peak in the breeding season and nearly 100% of deer >1 year old were pregnant.

Exact timing of estrus for individual does may be related to age (Cheatum and Morton 1946, Haugen 1975, Ozoga and Verme 1982, Langvatn et al. 2004), physical condition (Verme 1965), and past reproductive success (Mansell 1974, McGinnes and Downing 1977). Adults bred somewhat earlier (20 November) than yearlings (26 November) and 4 weeks earlier than fawns (18 December; Fig 1.3). Additionally, the

higher fecundity of early breeding adults is suggestive of an influence of physical condition on timing of estrus.

Historical Comparisons

There were no major differences in ovulation rates over 60 years in New Hampshire (Table 1.7). Similar to fawn pregnancy rates (Table 1.8), the ovulation rate of fawns was probably higher in 1981-1984 than 2011-2013, although the time periods were not statistically different. The lower fertility rates in 1951-1954 may be erroneous as these data were collected from deer harvested in December, when many may not have conceived; it is likely that these data underestimate the proportion of does ovulating (Siegler 1968).

Given the substantial increase in the deer population since the early 1980s, it was somewhat surprising that productivity of deer >1 year old remained stable from 1981-1987 to 2011-2013 (Table 1.8). The slight increases in adult and yearling pregnancy and fecundity in 2011-2013 were most likely attributable to more intensive examination of reproductive tracts during this study which allowed for more accurate determination of pregnancy during January and exclusion of deer from which fetuses may have been missing. It is possible that some deer killed in early winter, prior to implantation of embryos, were erroneously recorded as not pregnant during 1972-1987. Additionally, fetuses are occasionally ejected during motor vehicle collisions. At least 3 incomplete reproductive tracts (i.e., missing fetuses) were included in the 1981-1987 data and could not be censored because the number of fetuses attributable to them was not noted. It is possible that additional does with missing fetuses were included in the data, and unaccounted fetuses would reduce estimates of fecundity and birth rate. Only 1

unaccounted fetus per year would account for the 3-7% difference in birth rates; 11 deer collected from 2011-2013 were suspected to be missing ≥1 ejected or scavenged fetus.

It is also possible that extensive winter supplemental feeding of deer may have had a positive influence on overall herd health. Although some supplemental feeding probably occurred during the 1980s, it became far more prevalent through the 1990s and most deer in New Hampshire probably had access to supplemental feed during winter in 2011-2013 (Ross 2003; K. Gustafson, NHFG, personal communication). This could improve the nutritional status of wintering deer (Tarr and Pekins 2002) and potentially increase reproductive rates (Ozoga and Verme 1982). Supplemental feeding of a captive population did not increase the pregnancy rate of fawns (no fawns bred) but had the greatest influence on reproductive rates of yearlings (Ozoga and Verme 1982). Reproductive rates of yearlings in 2011-2013 in New Hampshire were relatively high and fawn pregnancy rates were low (Table 1.8).

The fawn pregnancy rate was 68% lower in 2011-2013 than in 1981-1987 (Table 1.8). Mild winters during 1981-1987 may have resulted in better conditioned fawns, allowing more to reach puberty and breed. Indeed, 3 of 5 pregnant fawns examined from 2011-2013 were collected in 2013 (Table 1.4); these fawns were born following the exceptionally mild winter of 2012. Deer densities were at their lowest point during the study period in the early 1980s, and this could also explain higher fawn pregnancy rates during that time. However, pregnancy rates during 2011-2013 in New Hampshire were consistent with recent fawn pregnancy rates in Vermont, Maine, and New Brunswick (see Chapter 3). Given the range of deer densities in these jurisdictions, it is more likely that

broader environmental factors (e.g., winter severity) have the greatest influence on fawn productivity.

The increase in potential recruitment from 1981-1987 to 2011-2013 was due almost entirely to a greater proportion of mature does in the 2011-2013 population. Management in most of New Hampshire has generally focused on increasing deer numbers by reducing the harvest rate of antlerless deer. Prior to 1983, hunters were allowed to harvest deer of either sex during the entire hunting season. Since then, harvest of female deer has been controlled by limiting the number of days of antlerless harvest. Much of the population increase since the early 1980s was due to conservative harvest rates of antlerless deer; as a result, more does survived to prime breeding age. Since adults are more fecund than yearlings or fawns, a higher proportion of adults results in a more productive population and an increase in potential recruitment.

The decline in observed recruitment (harvest fawn:doe ratio) suggests that summer fawn mortality increased from 1981-1987 to 2011-2013 (Fig 1.4). The difference between potential and observed recruitment likely overestimates fawn mortality because harvest fawn:doe ratios underrepresent the proportion of fawns in the population due to misidentification of fawns at reporting stations (K. Gustafson, NHFG, personal communication). Nonetheless, this should have been consistent over time and summer fawn mortality in 2011-2013 was probably >50%. Studies of fawn mortality in the northeast have found mortality rates ranging from 24% (Massachusetts; Decker et al. 1992) to 59% (Maine; Long et al. 1998), and a review of 19 studies from across the range of white-tailed deer found an average summer fawn mortality rate of 46% (Linnell et al.

1995). While summer fawn mortality has probably increased since the 1980s, the estimated mortality rate in 2011-2013 was typical of most white-tailed deer populations.

Coyote, black bear, and bobcat populations increased in New Hampshire from the 1980s to 2011-2013 (unpublished data, NHFG) and it is likely that predation of fawns has increased subsequently. Coyotes and black bears are known to be substantial predators of fawns (Long et al. 1998, Ballard et al. 1999, Patterson et al. 2002, Campbell et al. 2005, Carstensen et al. 2009) and could conceivably account for the observed decline in recruitment. However, it is also important to consider the potential influence of nutritional restriction during winter. Severe winter conditions that result in malnourishment of pregnant does can result in reduced birth weight and neonatal survival (Verme 1963, 1965, 1977), as well as reduced growth and survival during the nursing period (Therrien et al. 2008). Finally, the influence of hunter selectivity must be considered. Conservative antlerless harvest rates since 1983 meant that more mature does were available to hunters in 2011-2013 compared to 1981-1987, which may have allowed them to be more selective and avoid harvesting fawns (Coe et al. 1980) or does with fawns. Further, a long history of either sex hunting probably resulted in minimal selectivity by hunters during the early 1980s, but after 30 years of NHFG promoting reduced antlerless harvest as a means of increasing deer numbers, some hunters may now avoid harvesting fawns or does with fawns. If this was the case, it could account for some of the observed declines in both lactation rate and fawn:doe ratio.

Conclusions

The substantial increase in population density since the 1980s has not affected productivity of white-tailed deer in New Hampshire. In fact, productivity has increased due to a greater proportion of mature does in the population resulting from reduced antlerless harvest rates since the 1980s. Reasons for the decline in fawn pregnancy rate are not clear, but are potentially related to increasing density or a relatively higher frequency of severe winters since 2000. Regardless, the relative impact of reduced fawn productivity is minimal within the population, and on the whole, the increased density indicates that the deer population was likely below carrying capacity prior to harvest changes in the 1980s.

Both the decline in the fall lactation rate and the fawn:doe ratio in the harvest indicate that summer fawn mortality has increased. Multiple factors are likely responsible for declining recruitment including 1) population density in specific regions such as the Seacoast where density has more than tripled since the 1980s (unpublished data, NHFG), 2) winter severity that periodically reduces productivity, 3) direct predation of fawns by higher predator populations, and 4) gradual change in hunter selectivity. The additive impact of predation is difficult to estimate as it could be the proximate cause of death for malnourished fawns of does surviving severe winters. Likewise, measuring change in hunter selectivity since the 1980s is challenging, but any change would certainly bias recruitment indices based on harvested deer. A survey of hunter attitudes regarding the harvest of fawns and other antlerless deer would provide a better understanding of hunter selectivity and thereby improve the utility of these indices. Accurately measuring the impact of predation will require a field study to directly assess the causes of summer

fawn mortality. Importantly, despite declining over time, recruitment during 2011-2013 was still sufficient to allow for population growth and increased harvest during periods of average to below average winter severity.

CHAPTER II

INFLUENCE OF WINTER WEATHER ON NUTRITIONAL CONDITION OF WHITE-TAILED DEER IN NEW HAMPSHIRE

Introduction

White-tailed deer (*Odocoileus virginianus*) in New Hampshire are near the northern limit of their range where they regularly cope with severe winter conditions of deep snow, low temperatures, and limited mobility. Winter weather is often identified as the primary factor limiting the size of northern deer populations (Verme 1968), with survival influenced by winter severity and availability of winter habitat (Verme and Ullrey 1984). If winter weather is severe or if winter range is inadequate, significant mortality can occur and malnourishment of pregnant does can result in high neonatal mortality (Verme 1963, 1965, 1977, Ozoga and Verme 1982).

Fawns born to malnourished mothers are often smaller and have greatly reduced survival rates (Verme 1963, 1965, 1977), and this neonatal mortality may have the greatest impact on realized productivity (Mundinger 1981). Although proximate causes of neonatal mortality are variable, maternal malnutrition may be an important predisposing factor (Verme 1963, 1965, 1977). Studies of captive white-tailed deer have demonstrated that low birth-mass, depressed immunocompetence, and maternal rejection may predispose neonates to early mortality (Verme 1977, Sams et al. 1996). Nutritionally

deprived does may also allocate less energy to lactation resulting in reduced growth and survival of fawns (Therrien et al. 2008).

The welfare of deer across the northern portion of their range depends primarily on their winter nutritional status. The nutritional value of most winter browse is low-moderate compared to other seasonal foods (Ullrey et al. 1968, Mautz et al. 1976, Pekins and Mautz 1988), and deer are unable to meet their energy requirements from browse, even when available *ad libitum* (Mautz 1978). Thus, deer realize and are adapted to a negative energy balance in winter. White-tailed deer exhibit an annual weight cycle, gaining weight in spring, summer, and fall, and losing it throughout winter (Mautz 1978, Severinghaus 1981). Fat may account for >20% of an adult deer's total body weight prior to winter (McCullough and Ullrey 1983, Worden and Pekins 1995), and approximately 50% of the energy needed to survive winter can come from body reserves (Pekins and Tarr 2008). Fawns have less body fat than adults and are therefore more dependent on energy acquired from food resources (Tarr and Pekins 2002). Thus, length of winter, snow accumulation, and temperature are important factors influencing the extent of weight loss and ultimately survival.

In most ruminants fat can be considered a direct measure of physical condition (Riney 1955). Mammals store fat subcutaneously, in the omenta, around the kidneys and heart, and in the marrow (Harris 1945, Kistner et al. 1980). As nutritional condition declines, subcutaneous fat is catabolized first, followed by omental, renal, pericardial, and finally marrow (Harris 1945, Kistner et al. 1980). Female deer reach peak levels of stored body fat shortly after conception and lose fat throughout winter and into the nursing period (Scanlon et al. 1976, Worden and Pekins 1995). The rate of fat loss is

related to winter severity and forage consumption as well as the number of fetuses (Cothran et al. 1987). In any measure of fat reserves, younger individuals should be expected to be in poorer condition because they allocate more of their energy to growth and their metabolic costs are higher proportionally (Verme and Ozoga 1980). Because northern deer exhibit an annual cycle of fat deposition and depletion and the various fat stores are used in a predictable sequence, measurements of these reserves can provide a reasonable estimate of nutritional status.

Another important and often overlooked factor influencing condition of white-tailed deer is stress. Glucocorticoids are released by the adrenal cortex in response to environmental, physiological, or psychological stressors; glucocorticoids increase the rate of gluconeogenesis in the liver, increase protein catabolism, and mobilize fat reserves (Asterita 1985). Chronic stress causes prolonged glucocorticoid activity which continually diverts energy away from processes that are not required for immediate survival such as growth, reproduction, and immune system responses (Munck et al. 1984, Sapolsky 2002); therefore, chronic stress is closely related to an individual's nutritional condition (Saltz and White 1991a). Nutritional condition is often assessed by measuring an animal's energy reserves, but it is stress which mediates the rate at which these reserves are utilized (Saltz and White 1991a); consequently, measurement of glucocorticoid levels should provide additional insight into the energy status of individuals as well as the population.

Management of northern deer populations requires appraisal of annual winter mortality and commensurate adjustment of harvest rates. Rather than conduct extensive dead deer surveys which are expensive and rarely provide reliable estimates over large

areas, a practical alternative is to monitor winter conditions and use a winter severity index (WSI) to estimate winter losses. Winter mortality rate, body condition, fetal growth, and neonatal mortality are related to winter severity (Verme 1977, MDIFW 2007). Most states and provinces across northern deer range calculate a WSI; common measurements include ambient temperature, snow depth, and deer sinking depth. The New Hampshire Fish and Game Department (NHFG) uses a simple WSI which sums the number of days with snow depth >46 cm and the number of days with minimum temperature <-18 °C; a similar WSI is used in several other states (e.g., Minnesota, Vermont, Wisconsin). Typically, WSI is used as a relative index because the relationship between WSI and actual winter mortality may vary among jurisdictions, or even among individual deer wintering areas. The median statewide WSI in New Hampshire was 35, ranging from 13-101 in 1980-2013; generally, WSI >50 resulted in population declines (unpublished data, NHFG).

While a WSI is a reasonable predictor of winter mortality, managers must still use discretion when interpreting the effects of winter weather on herd dynamics. In addition to temperature and snow depth, duration and timing of severe winter conditions, population density, and quality and availability of winter habitat are also important factors. Widespread supplemental feeding of deer during winter now occurs throughout New Hampshire and is particularly prevalent in northern areas. Ross (2003) suggested that most deer in New Hampshire probably have access to supplemental feed that can influence the energy balance of deer during winter (Tarr and Pekins 2002), confounding the interpretation and use of a WSI.

Accurately predicting the effects of winter weather on New Hampshire's deer population requires that additional and current data be collected to assess the validity and use of the WSI. This study evaluated the use of marrow fat and fecal glucocorticoids as indicators of winter condition of deer and examined the influence of winter duration, snow depth, temperature, and reproductive status on nutritional condition and stress of wintering white-tailed deer in New Hampshire.

Methods

Biological samples were collected from winter deer mortalities from late December through mid-May in 2010-2011, 2011-2012, and 2012-2013; this time frame coincides with the gestation period for white-tailed deer in New Hampshire. Necessary biological samples or whole carcasses were collected by NHFG or University personnel and frozen until later processing. Each deer was identified by a unique identification number, kill date, and location. Biological samples collected from each deer included a central incisor, the reproductive tract, femur marrow, and feces.

The study area was divided into three regions based on similarities in deer density, habitat quality, and winter severity. The North region consists of NHFG wildlife management units (WMUs) A, B, C1, C2, D1, D2E, E, F, and G2, the South region consists of WMUs D2W, G1, H1, H2, I1, I2, J1, J2, and K, and the Seacoast region consists of WMUs L and M (Fig. 1).

Deer were aged based on tooth replacement and wear techniques (Severinghaus 1949) and cementum annuli analysis from an extracted central incisor (Gilbert 1966, Low and Cowan 1963); cementum analysis was performed by Matson's Laboratory (Milltown,

Montana). Tooth replacement and wear was used to distinguish fawns from deer >1 year old and to age deer not aged by cementum analysis. For most analyses deer were grouped into 3 age classes; fawn (0.5-1 year old), yearling (1.5-2 years old), and adult (>2.5 years old).

Marrow Collection and Processing

A plug of marrow (>2 g; $\bar{x}$ = 7.1 g, σ = 4.1 g) was collected from the central portion of the femur, placed in an airtight plastic bag, and frozen until processing. Marrow samples were processed soon after they were received to avoid effects of prolonged freezing; water loss from prolonged freezing can result in up to 10% higher estimates of fat content (Greer 1968). Samples were oven-dried to constant weight to determine the percent fat in the marrow (MF; Neiland 1970).

The measurement of % fat in bone marrow (Harris 1945, Cheatum 1949b) is commonly used to assess nutritional status. Marrow from any long bones or mandibles can be used, but results may not be directly comparable as fat is mobilized more quickly in proximal bones and femur marrow is used most commonly (Cheatum 1949b, Fuller et al. 1986, Davis et al. 1987). Because marrow fat accounts for only 2-3% of the stored body fat in white-tailed deer (McCullough and Ullrey 1983) and is the last fat reserve catabolized (Harris 1945), this technique is a one-way indicator; loss of any fat indicates poor condition, but high levels of fat do not necessarily indicate good condition (Mech and DelGiudice 1985).

Fecal Sampling

Fecal samples (>10 pellets) were collected from the lower portion of the colon following removal of the reproductive tract; samples were collected during 2011-2012

and 2012-2013 only. Feces were collected from as near the anus as possible to avoid potentially elevated glucocorticoid levels in newer feces resulting from the traumatic nature of the animal's death. In order to evaluate the potential influence of collecting feces from dead deer, fecal samples were also collected from 3 captive deer (Holderness, NH and Gray, ME) for comparison. Fecal samples were placed in individually labeled airtight plastic bags and frozen (-20 °C) until assay. Because there were no obvious differences in fecal consistency, samples were not dried; drying or lyophilizing samples does not affect the concentration of hormone metabolites if there are no differences in consistency (Möstl and Palme 2002). Glucocorticoid levels in the feces represent an aggregation of glucocorticoids and their metabolites over the previous 12-24 h (Millspaugh et al. 2002), and therefore tend to be more stable and indicative of chronic stress (Kaey et al. 2006). Previous studies with ungulates (e.g., Millspaugh et al. 2002, Creel et al. 2009) have confirmed the reliability of estimating stress levels using fecal glucocorticoids (fGC).

Glucocorticoid Extraction and Enzyme Immunoassay

Fecal samples were homogenized and 0.50 g (±0.05 g) of well-mixed wet feces was placed into extraction tubes with 5.0 mL of 80% methanol and shaken mechanically (~1 h) for extraction. The contents were allowed to settle and samples were then centrifuged (1600 rpm, 20 min, 25 °C). The supernatant was transferred into clean tubes and extracts were stored at -20 °C until assay. For assay purposes, extracts were diluted 1:16 in assay buffer; some samples were diluted 1:31 in order to fall within the detection range of the assay. The concentration of fGCs in each sample was determined using a cortisol enzyme immunoassay (EIA) kit (Assay Designs, Ann Arbor,MI); all hormone

measurements were carried out in duplicate. Concentrations were determined as ng/mL then divided by the mass of feces extracted to express the results as ng/g of wet feces. Binding curves for serial dilution of extracts and cortisol standards were parallel from 156–10,000 pg/mL. Intra-assay coefficient of variation was 4.69%. Sensitivity of the assay was 0.06 ng/mL (the lowest concentration detectable); this was >2 orders of magnitude below the minimum concentration of diluted fecal extracts. This EIA has not been biologically validated for white-tailed deer, but was used previously for fGC analysis with elk (*Cervus elaphus*; Forristal et al. 2012).

Winter Severity Data

The WSI used by NHFG sums the number of days with snow depth ≥46 cm (18 in) and the number of days with minimum temperature ≤-18 °C (0 °F) from 1 December–30 April. It is estimated that deer do not need to increase metabolism to maintain body heat when temperatures are above -10 °C (Mautz et al. 1992), and heat produced during digestion of browse may effectively reduce this temperature by about 10 °C (Jensen et al. 1999). Deer movement becomes restricted at snow depths between 40-50 cm (Drolet 1976). Thus, this WSI provides a reasonable approximation of conditions that induce higher energetic costs.

Snow depth and temperature data were collected at 15 NOAA weather stations located throughout the state and monthly summary data was obtained by NHFG. Data from multiple stations was averaged based on geographic location to calculate WSI values for each wildlife management unit (WMU; Appendix B); values for all WMUs were averaged to determine a statewide WSI. This index has been calculated by NHFG since 1965.

Since only monthly summaries were available from NHFG, data from 55 NOAA weather stations (including the 15 stations used by NHFG; NCDC 2013) located throughout New Hampshire were used to estimate a cumulative WSI for each day of winter. This allowed for an estimate of WSI through the date of an animal's death. Similar to the NHFG calculation, data were averaged based on geographic location to calculate WSI values for each WMU (Appendix B). The WSI value for each WMU was used for all deer killed in that WMU. The total WSI values calculated using all 55 NOAA stations were very similar to WSI values calculated by NHFG ($r = 0.92$, $P < 0.001$).

Statistical Analyses

To evaluate the nutritional status of the deer population through winter, the proportion of deer collected each month with MF <80% was analyzed using the Cochran-Armitage trend test; MF ≥80% generally indicates no loss of MF (Greer 1968). Data were not pooled in this way for other statistical analyses because uneven distribution of samples limited statistical power. Yearlings and adults were combined for several analyses due to low yearling sample size. Actual MF values were log-transformed to account for the substantial skew toward higher values; transformed data were analyzed via linear regression and analysis of covariance (ANCOVA) to explore differences in the rate of loss of marrow fat among years, regions, and age classes. To validate the use of fGC as a measure of winter nutritional condition, linear regression analysis was used to evaluate relationships between MF and fGC, and winter progression and fGC. Wilcoxon or Kruskal-Wallis rank tests were used to identify differences in fGC between years and among regions and age classes. Analyses were conducted in JMP 10 (SAS Institute Inc. 2007).

The influence of winter progression (Julian days beginning 1 December), winter severity, reproductive status, and age on overwinter variation of fGC and MF was explored using generalized linear mixed regression models (GLMM) using the *lme4* package (Bates et al. 2012) in R (R Development Core Team 2011). Model parameters included day of winter (beginning 1 December), WSI, number of fetuses, breeding date, and age class; year and region were included as random effects in all models (Table 2.1). Sixteen competing models were developed to explain MF of all age classes; 16 different competing models were developed to explain MF of yearlings and adults only which allowed for inclusion of reproductive parameters. Similarly, 16 competing models were developed to explain fGC; MF was also included as a parameter in these models (Table 2.1). The best fitting models were determined by using the lowest second-order Akaike Information Criterion (AIC_c) scores with the *AICcmodavg* package (Mazerolle 2012) in R. Models with shared AIC_c weight and ΔAIC_c scores <2 were averaged using the *MuMIn* package (Barton 2013) in R; model averaging can lead to more precise parameter estimates (Burnham and Anderson 2002, Bolker et al. 2008).

Table 2.1. Variables used in generalized linear mixed effects models to explain marrow fat content and fecal glucocorticoid concentration in white-tailed deer during December–May in New Hampshire, 2011-2013.

Explanatory Variable	Effect	Parameters	Type
Year	Random	2011-2013	Categorical
Region	Random	North, South, Seacoast	Categorical
Age class	Fixed	Fawn, Yearling, Adult	Categorical
Winter severity (WSI)	Fixed	0-91	Numerical
Day of winter	Fixed	19-170	Numerical
Fetuses[1]	Fixed	0-3	Numerical
Breeding day (Julian day)[2]	Fixed	309-374	Numerical
Marrow fat[3]	Fixed	1.4-95.4%	Numerical

[1] Only included in marrow fat models

[2] Only included in marrow fat models for deer >1 year old

[3] Only included in fecal glucocorticoid models

Results

Winter severity in 2010-2011 was moderately severe with a WSI of 61, the 6th most severe since 1980, with deep snow persisting throughout the state for several months. Conversely, mild conditions in winter 2011-2012 with WSI of 13, the lowest since NHFG began tracking WSI in 1965, afforded deer near continuous mobility, broad access to natural foods, and less reliance, restriction, and use of traditional wintering areas and supplementary feeding sites. Winter 2012-2013 was also mild, with the 4th lowest WSI (16) since 1980. All 3 winters were more severe in the North (WSIs of 74, 23, and 25) than the South (50, 5, 9) and Seacoast (44, 2, 7). Only WMU A (2) accumulated any WSI points for snow depth in 2012, and 13 (65%) WMUs accumulated 0 WSI points for snow depth in 2013.

Marrow Fat

Marrow samples were collected from 174 deer: 52 (30%) fawns, 16 (9%) yearlings, and 106 (61%) adults. More samples were collected in 2010-2011 (n = 91) than in 2011-2012 (n = 38) or 2012-2013 (n = 45; Table 2.2). Samples were collected from every WMU except D2E; 64 samples were collected from the North, 79 from the South, and 30 from the Seacoast. The Seacoast included a greater proportion of fawns (43%) than the South (30%) or North (22%).

The range of MF across all years was 1.4-95.4%. The majority (>83%) of deer >1 year old showed no/minimal MF loss (≥80% MF) in January and February, dropping to 38% in April ($P = 0.012$). The proportion of fawns showing no loss of MF declined from 76% in January to 38% in February; all fawns collected in April and May lost MF ($P < 0.001$; Fig. 2.1). There were no differences in the rate of MF loss among age classes

Table 2.2. Marrow fat samples collected from female white-tailed deer in New Hampshire, December–May, 2010–2013. Age was determined by cementum annuli analysis or tooth replacement and wear.

	2011	**2012**	**2013**	**Total**
Fawn	20 (22%)	15 (39%)	17 (38%)	52 (30%)
Yearling	9 (10%)	4 (11%)	1 (2%)	14 (8%)
Adult	62 (68%)	19 (50%)	27 (60%)	108 (62%)
Total	91	38	45	174

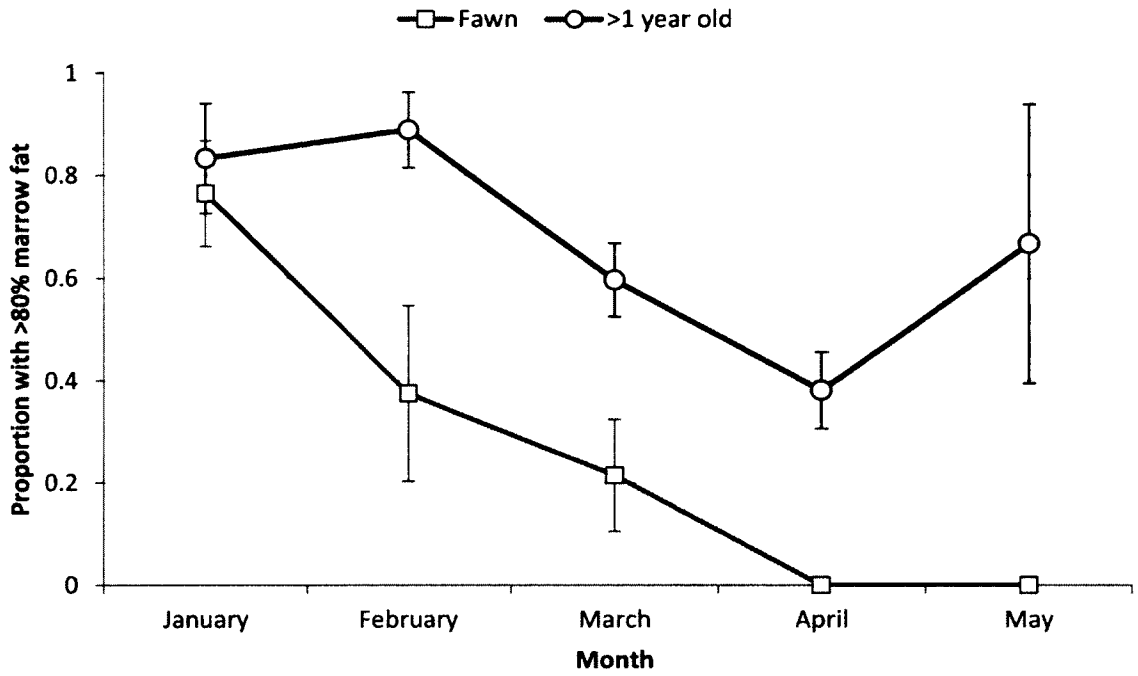

Figure 2.1. Proportion of female white-tailed deer with ≥80% marrow fat during January–May, 2011–2013. Marrow fat content <80% indicates depletion of energy reserves and poor nutritional condition. All fawns and most deer >1 year old collected after 1 April were in poor condition. Error bars show SE.

($P = 0.20$), but fawns began losing MF earlier than deer >1 year old ($P < 0.001$). In 2011, deer from the North lost MF faster than deer from the South or Seacoast ($P = 0.009$); there were no differences among regions in 2012 or 2013 (Fig 2.2), albeit sample sizes were smaller. There were no differences in the rate of MF loss among years for any age class; however, all age classes declined fastest in 2011.

Sixteen competing models were tested to explain differences in MF; parameters of the top model included age class, day of winter, WSI, and number of fetuses. The lowest MF was observed in fawns, later in winter, and in deer that had experienced greater WSI (Table 2.3). Sixteen models were tested to explain differences in MF of deer >1 year old only. Lower MF was observed later in winter, in deer that had experienced greater WSI, and in deer that conceived earlier and carried more fetuses (Table 2.4).

Fecal Glucocorticoids

Fecal samples were collected from 62 deer: 23 (37%) fawns, 6 (10%) yearlings, 32 (52%) adults, and 1 (2%) of unknown age. A similar number of samples was collected in 2012 (n = 29) and 2013 (n = 33); more fawns were sampled in 2012 (14, 48%) than 2013 (9, 27%; Table 2.5). More samples were collected in the North (n = 33) than the South (n = 22) or Seacoast (n = 6). Differences in regional sample size were most pronounced in 2013 when 67% of all samples were collected in the North.

Concentrations of glucocorticoids ranged from 145-3297 ng/g of feces. Median fGC was 684 ng/g, 68% were <1000 ng/g, and 34% were <400 ng/g. The 3 samples from live, captive deer had fGCs from 101-202 ng/g. There was no temporal trend in fGC through winter ($\beta = -3.55$, $R^2 = 0.02$, $P = 0.27$; Fig 2.3) and there were no differences ($P > 0.05$) among age classes or regions. There was no difference between years, although

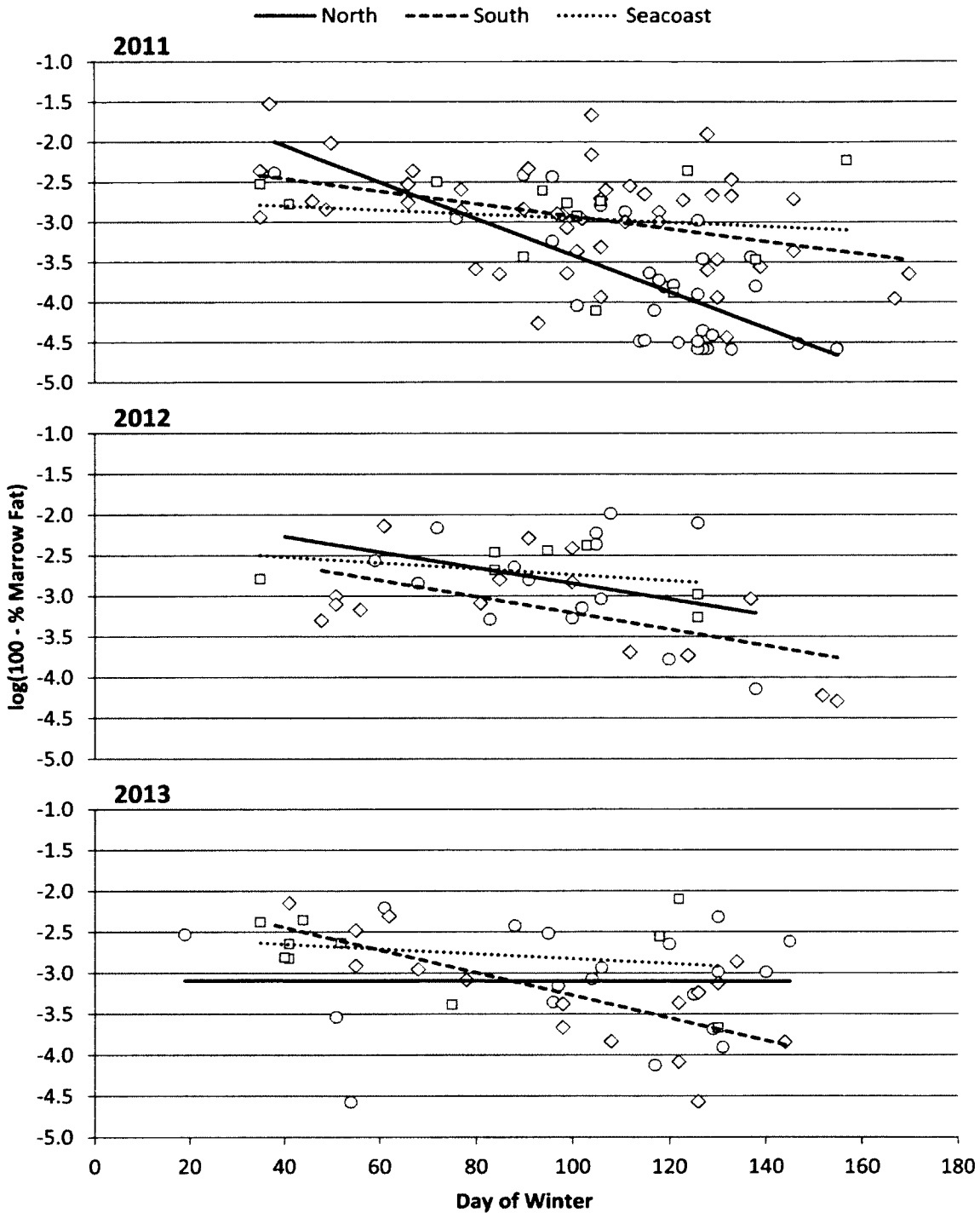

Figure 2.2. Differences in the rate of marrow fat loss for deer collected in the North (circles), South (diamonds), and Seacoast (squares) regions during 2011, 2012, and 2013. Deer from the North lost fat faster than the other regions in 2011; there were no differences among regions in 2012 or 2013. Marrow fat values are log-transformed. The first day of winter is 1 December of the prior year, 1 April is day 121.

Table 2.3. Comparison of 16 models of marrow fat content of white-tailed deer during December–May developed from age, winter duration (DOW), winter severity (WSI), and reproductive data from New Hampshire, 2011-2013. The fawn age class, winter duration and WSI were indicated as important factors in the top model.

Model	K	AIC_c	ΔAIC_c	w_i	LL
Age, fetuses, DOW, WSI	9	1285.1	0.0	1.00	-632.92
Fetuses, DOW, WSI	7	1300.1	15.0	0.00	-642.64
Age, fetuses, WSI	8	1302.6	17.5	0.00	-642.81
Age, fetuses, DOW	8	1307.7	22.6	0.00	-645.36
Fetuses, WSI	6	1314.7	29.6	0.00	-651.08
Fetuses, DOW	6	1323.1	38.0	0.00	-655.28
Age, fetuses	7	1351.7	66.5	0.00	-668.44
Fetuses	5	1364.2	79.1	0.00	-676.90
Age, DOW, WSI	8	1506.7	221.5	0.00	-744.89
Age, WSI	7	1516.7	231.6	0.00	-751.00
Age, DOW	7	1529.0	243.8	0.00	-757.14
DOW, WSI	6	1543.8	258.7	0.00	-765.65
WSI	5	1545.4	260.2	0.00	-767.51
DOW	5	1562.6	277.4	0.00	-776.11
Age	6	1568.5	283.3	0.00	-777.98
intercept only	4	1589.8	304.7	0.00	-790.78

Model coefficients:	Estimate	SE	z	Pr(>|z|)
(Intercept)	110.375	6.982	15.808	<0.001
Day of winter	-0.279	0.051	-5.432	<0.001
WSI	-0.301	0.057	-5.243	<0.001
Fetus	3.529	2.477	1.424	0.156
Age (fawn)	-16.588	5.490	-3.022	0.003
Age (yearling)	-5.488	4.787	-1.146	0.254

Table 2.4. Comparison of 16 models of marrow fat content of deer >1 year old during December–May developed from winter duration (DOW), winter severity (WSI), and reproductive data from New Hampshire, 2011-2013. Parameter estimates for top models (ΔAIC_c <2) were averaged using the *MuMIn* package in R. Winter duration and WSI were indicated as important factors in the top models.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_i**	**LL**
Breed date, fetuses, WSI	7	813.5	0.0	0.68	-399.09
Breed date, fetuses, DOW, WSI	8	815.0	1.5	0.32	-398.66
Breed date, fetuses, DOW	7	831.1	17.6	0.00	-407.91
Breed date, fetuses	6	834.1	20.6	0.00	-410.56
Breed date, WSI	6	868.6	55.1	0.00	-427.84
Breed date, DOW, WSI	7	869.3	55.9	0.00	-427.06
Breed date, DOW	6	885.0	71.6	0.00	-436.07
Breed date	5	889.2	75.7	0.00	-439.28
Fetuses, WSI	6	901.1	87.6	0.00	-444.10
Fetuses, DOW, WSI	7	902.0	88.5	0.00	-443.40
Fetuses, DOW	6	917.9	104.4	0.00	-452.51
Fetuses	5	924.9	111.4	0.00	-457.12
WSI	5	1075.8	262.3	0.00	-532.63
DOW, WSI	6	1079.6	266.1	0.00	-533.41
DOW	5	1095.7	282.3	0.00	-542.61
intercept only	4	1100.8	287.3	0.00	-546.24

Model-averaged coefficients:	**Estimate**	**SE**	**z**	**Pr(>|z|)**
(Intercept)	134.872	50.936	2.648	0.008
Breed day	-0.147	0.150	0.985	0.325
Fetus	2.841	3.149	0.902	0.367
WSI	-0.336	0.100	3.378	<0.001
Day of winter	-0.155	0.071	2.181	0.029

Table 2.5. Fecal samples collected from female white-tailed deer in New Hampshire, December–May, 2011–2013. Age was determined by cementum annuli analysis or tooth replacement and wear.

	2012	**2013**	**Total**
Fawn	14 (48%)	9 (27%)	23 (37%)
Yearling	3 (10%)	2 (6%)	5 (8%)
Adult	12 (42%)	21 (64%)	33 (53%)
Unknown		1 (3%)	1 (2%)
Total	29	33	62

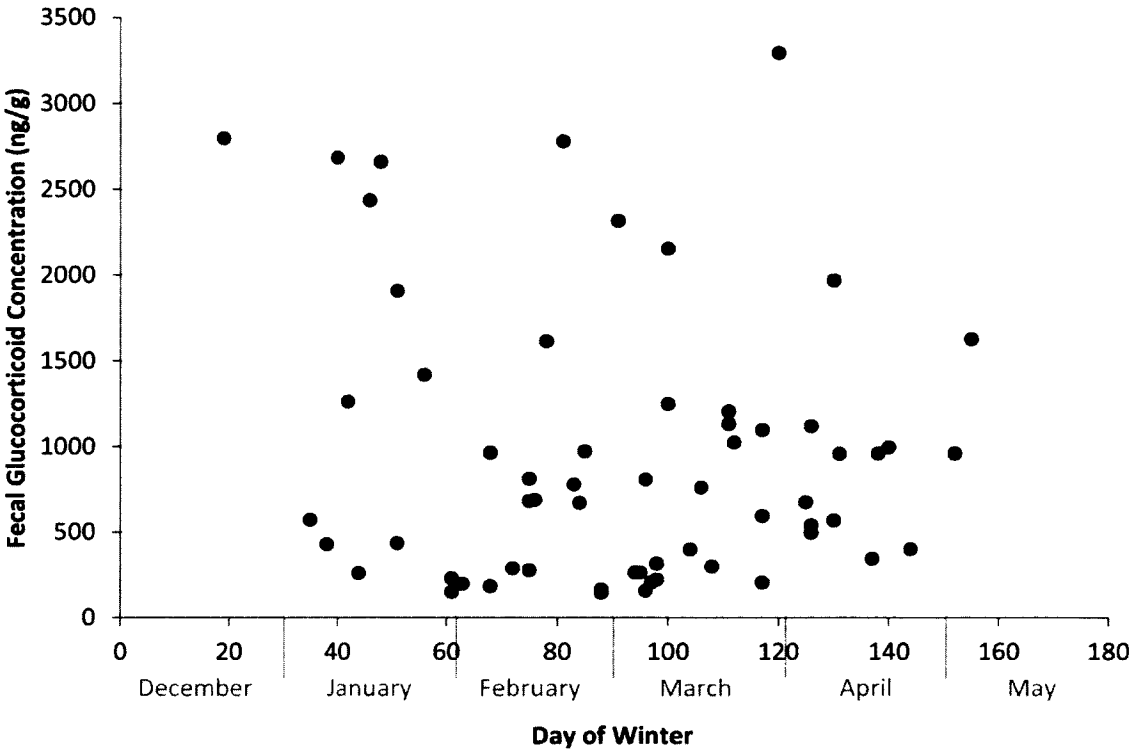

Figure 2.3. Seasonal pattern of fecal glucocorticoid concentrations in female white-tailed deer (n = 62) during winter in New Hampshire, 2012–2013. The first day of winter is 1 December, 1 April is day 121.

median fGC in 2012 (958 ng/g) was 69% higher than 2013 (567 ng/g; $P = 0.17$). Both marrow and fecal samples were collected from 42 deer; including 23 in 2012 and 19 in 2013. There was no relationship between MF and fGC ($\beta < 0.001$, $R^2 < 0.001$, $P = 0.86$; Fig 2.4).

Sixteen competing models were tested to explain differences in fGC. Parameters of the top model included age class, day of winter, WSI, and MF; however, the effect of each parameter was relatively weak and poorly determined (Table 2.6). These results suggest that none of these factors are useful predictors of fGC.

Discussion

Fecal glucocorticoids

Winter is a period of chronic stress for northern white-tailed deer as they must endure low temperatures, deep snow, and reduced food quality and quantity (Ullrey et al. 1964). Chronic stress causes prolonged glucocorticoid activity and is closely related to an individual's nutritional condition (Saltz and White 1991a, Sapolsky 2002). However, there was no relationship between fGC and MF (Fig 2.4) and there was no apparent temporal trend in fGC through winter (Fig 2.3). Further, none of the parameters in the top fGC model were significant and most were poorly determined (Table 2.6), suggesting fGC may not be a useful predictor of poor nutritional condition of deer during winter.

Seasonal variation of glucocorticoid levels with peak values during winter has been reported in white-tailed deer (Bubenik et al. 1983), mule deer (*Odocoileus hemionus*; Saltz and White 1991a), and red deer (*Cervus elaphus*; Huber et al. 2003).

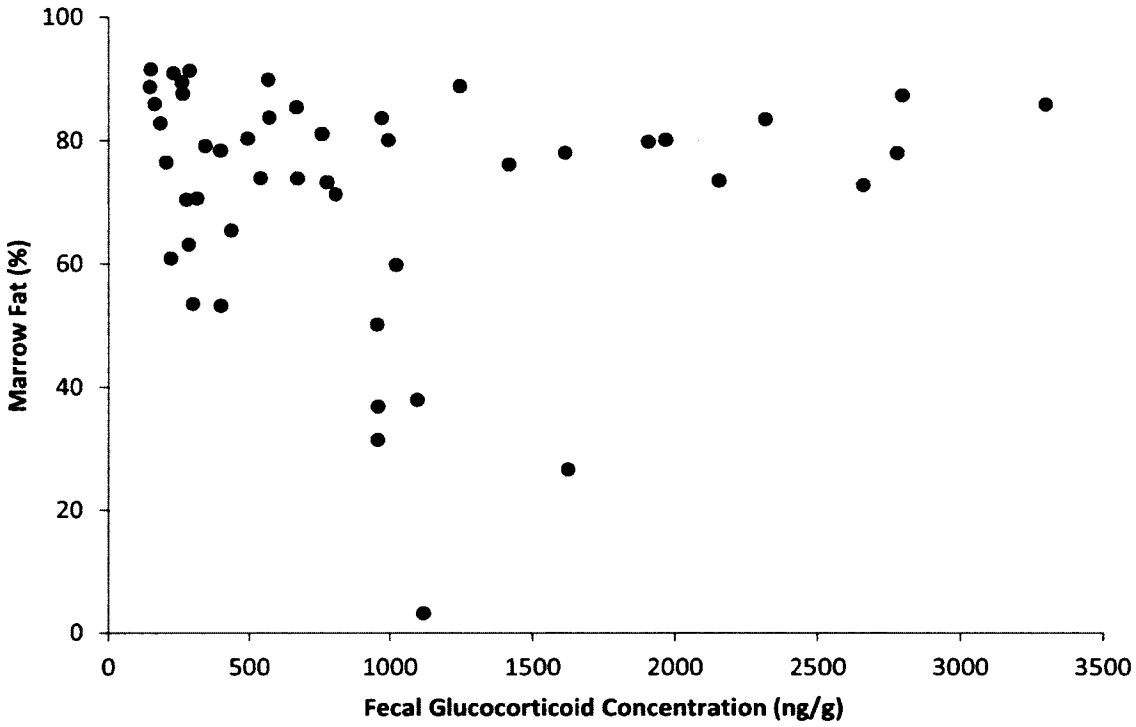

Figure 2.4. Relationship between fecal glucocorticoid concentration and marrow fat content of 42 female white-tailed deer killed during December–May, 2012–2013 in New Hampshire.

Table 2.6. Comparison of 16 models of fecal glucocorticoid concentration in white-tailed deer during winter developed from age, winter duration (DOW), winter severity (WSI), and marrow fat content (FMF) from New Hampshire, 2012-2013. None of the parameters in the top model were useful predictors of fecal glucocorticoid concentrations.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_i**	**LL**
Age, FMF, DOW, WSI	8	694.8	0.0	0.81	-337.40
Age, FMF, WSI	7	697.7	2.9	0.19	-340.31
Age, FMF, DOW	7	714.4	19.6	0.00	-348.73
FMF, DOW, WSI	6	716.8	22.0	0.00	-351.28
FMF, WSI	5	719.5	24.7	0.00	-354.00
Age, FMF	6	733.2	38.4	0.00	-359.57
FMF, DOW	5	736.4	41.6	0.00	-362.47
FMF	4	755.2	60.4	0.00	-373.14
Age, DOW, WSI	8	925.1	230.3	0.00	-453.12
Age, WSI	7	927.4	232.6	0.00	-455.65
Age, DOW	7	944.8	250.0	0.00	-464.36
DOW, WSI	5	960.3	265.5	0.00	-474.59
WSI	4	963.0	268.2	0.00	-477.13
Age	6	963.5	268.7	0.00	-474.99
DOW	4	980.1	285.3	0.00	-485.71
intercept only	3	999.2	304.4	0.00	-496.40

Model coefficients:	**Estimate**	**SE**	**z**	**Pr(>|z|)**
(Intercept)	1920.978	1113.358	1.725	0.092
KDOW	-4.258	5.120	-0.832	0.411
FMF	-6.604	9.244	-0.714	0.479
WSI	1.197	13.937	0.086	0.932
Age (fawn)	-171.426	313.197	-0.547	0.587
Age (yearling)	-94.144	484.199	-0.194	0.847

Additionally, cortisol levels in mule deer fawns increased substantially in the last few weeks prior to death from starvation (Saltz and White 1991b). However, Taillon and Cote (2008) found a similar lack of temporal trend in fGC through winter for fawns on Anticosti Island and suggested that deer may be able to suppress the stress response in order to withstand harsh winter conditions.

It is also possible that the extreme variability of fGCs observed in this study inhibited detection of any relationships. The lower fGC values from live, captive deer were likely due to sample collection during summer and fall when glucocorticoid concentrations are lower (Bubenik et al. 1983, Huber et al. 2003). However, it is also possible that some of the highest fGC values observed in this study were erroneous. Cause of death for most study animals was traumatic (motor vehicle collision or predation) and may have caused a spike in glucocorticoid levels if the animal did not die immediately. Measurement of levels in feces was an attempt to avoid these spikes, but internal damage likely resulted in many samples being contaminated with blood. Because sampling was opportunistic, some carcasses or samples remained unfrozen for several days. Under those conditions, it is possible that microbial metabolism of glucocorticoids resulted in substantial increases in fGC (Washburn and Millspaugh 2002) which could explain some of the extremely high values observed.

This noninvasive technique has great potential for measuring stress in free-ranging deer, and the results of this study should not deter additional research in this area. Future studies will need to be carefully designed and conducted under more controlled circumstances. Collection of feces in the field would likely avoid many of these issues,

and the data could still be easily related to weather conditions or other factors known to influence nutritional condition of deer.

Marrow fat

Only 8 study animals died of causes other than motor vehicle collision, so meaningful comparison of MF among causes of death was not possible. Fawns were sampled in similar proportions to those observed in the harvest, suggesting they were not over- or underrepresented; however, both could exhibit a similar bias relative to the population. The low proportion of yearlings (8%) and relatively high proportion of deer ≥9 years old (22%) suggests a bias toward older deer. This age distribution is unrealistic for an exploited and growing population such as New Hampshire's, so it is likely that many of these older deer were in poor condition. Roadkilled deer may be biased toward poorly conditioned individuals, as they may be less willing or able to move from plowed roadways (O'Gara and Harris 1988). There were no obvious differences in MF between deer 1-8 years old and deer ≥9 years old; however, high MF values do not necessarily indicate good condition (Mech and DelGiudice 1985). Because MF accounts for only 2-3% of the stored body fat in white-tailed deer (McCullough and Ullrey 1983) and is the last fat reserve catabolized (Harris 1945), an individual may have lost most of its body fat and still have a high percentage of MF (Ransom 1965). Many of these older deer may also have been debilitated in some way (i.e., injured, sick, parasitized, or simply old) but had not yet depleted their energy reserves. Regardless, the presence of a bias should not have altered how the various factors affected MF, though it could limit inference about the nutritional status of the population.

As winter progressed, the proportion of deer that were in poor nutritional condition (MF <80%) increased (Fig 2.1). This was expected given that white-tailed deer exhibit an annual weight cycle (Mautz 1978, Severinghaus 1981) because the nutritional value of most winter browse is low-moderate compared to other seasonal foods (Ullrey et al. 1968, Mautz et al. 1976, Pekins and Mautz 1988), and deer are unable to meet their energy requirements from browse, even when available *ad libitum* (Mautz 1978). Fat may account for >20% of a deer's total body weight prior to winter (McCullough and Ullrey 1983, Worden and Pekins 1995), and approximately 30-50% of the energy needed to survive winter can come from body reserves, with the remainder acquired from food resources (Mautz 1978, Pekins and Tarr 2008). Thus, deer realize and are adapted to a negative energy balance in winter.

All ages lost MF at a similar rate (Fig 2.1), but fawns began losing MF earlier than deer >1 year old and all fawns collected after 1 April had MF <80%, indicating they had depleted most of their energy reserves and were in poor nutritional condition. Fawns enter winter with <15% body fat (Tarr and Pekins 2002) because they allocate much of their energy to growth (Verme and Ozoga 1980) and their smaller body size makes them more susceptible to severe winter conditions; however, differences in thermoregulatory costs are small (Jensen et al. 1999) and use of packed trails in wintering areas likely minimizes locomotion costs associated with deep snow (Pekins and Tarr 2008). Fawns also have proportionally higher energy requirements than older deer (Kanter 1989, Jensen et al. 1999) and must obtain a greater proportion of their energy from forage intake (Pekins and Tarr 2008). However, most deer in New Hampshire have access to supplemental food during winter (Ross 2003) which may disproportionately improve

nutritional condition of fawns (Tarr and Pekins 2002). These factors could effectively minimize differences in energy costs between fawns and older deer. Additionally, Since MF is such a small percentage of a deer's energy reserves and there can be substantial individual variation, differences in the rate of fat loss between fawns and adults could be difficult to detect using this measure. Nonetheless, fawns deplete their energy reserves earlier than older deer and consistently experience greater mortality as a result, regardless of weather conditions.

Interestingly, the proportion of deer >1 year old in poor condition after 1 April did not vary among years despite substantial differences in WSI; 63, 67, and 57% collected after 1 April had lost some MF in 2011, 2012, and 2013, respectively. While loss of body fat is expected, loss of MF indicates depletion of major energy reserves (Harris 1945, Kistner et al. 1980), demonstrating the strong influence of winter duration and the associated negative energy balance on nutritional condition, regardless of weather conditions. Indeed, the models indicate day of winter as the primary factor affecting MF. Based on parameter estimates for all age classes (Table 2.3), WSI would have accounted for only 35% of fat loss through 1 April in 2011 (WSI = 61) and only 10% in 2012 (WSI = 13) for an adult carrying twins; the remainder was attributable to how late in winter the deer was killed.

Low temperature and deep snow increase energetic costs for wintering deer; deep snow in particular increases locomotion costs, restricts access and availability of food (Dumont et al. 2005), and is associated with high mortality (Moen 1976, Mautz 1978). Winter weather accounted for substantial loss of MF in 2011, and a greater proportion of all deer had MF <10% in 2011 (12%) than in 2012 (0%) or 2013 (4%; Appendix C). It is

not clear if a minimal MF level ensures mortality, but MF <10% is likely indicative of eventual death (Franzmann and Arneson 1976). Although deer may deplete most of their energy reserves during winter regardless of weather conditions, the WSI may be the best indicator of annual variation in winter mortality.

Among the components of WSI, the number of days with minimum temperature <-18 °C does not vary substantially from year to year, whereas the number of days with snow depth >46 cm can vary greatly, and actual snow depth even more so (NCDC 2013). Garroway and Broders (2005) found that snow depth was the primary factor affecting body condition of deer during winter in Nova Scotia, although they did not consider the date of the animal's death in their analyses. Total WSI proved to be a better predictor than either component independently; however, the lack of substantial snow accumulation during 2012 and 2013 and resultant lack of WSI points from snow depth limited an independent analysis of the snow depth and temperature components. Nonetheless, duration of deep snow is probably the primary factor in the WSI affecting nutritional condition and overwinter survival of white-tailed deer in New Hampshire.

Deep snow that limits forage availability should have the greatest influence on condition of fawns because they obtain a greater proportion of their energy from forage intake (Pekins and Tarr 2008). Timing of deep snow is also critical to its impact on nutritional condition and survival, but is not captured in the WSI. Deep snow during January will have little impact on nutritional condition as most deer still have adequate energy reserves at that time. Conversely, lasting deep snow in April when most deer have depleted their energy reserves would elevate mortality regardless of the overall WSI.

Timing of spring green-up is also critically important to survival of northern white-tailed deer, which are adapted to withstand 90-100 days of negative energy balance (Worden and Pekins 1995). All fawns and most adults had depleted their energy reserves by 22 April (Fig 2.1), the average date of green-up in New Hampshire (Pekins et al. 1998), and recovery of these deer is dependent on improved nutritional intake associated with green-up and movement out of deer wintering areas. Substantial mortality often occurs if winter conditions persist well into April and green-up is delayed (K. Gustafson, NHFG, personal communication). Timing of green-up is particularly important for pregnant does because energy costs of gestation increase rapidly during this time. Energy costs associated with gestation are minimal during the first two trimesters, with about 90% of the total occurring in the final trimester; assuming the final trimester begins 1 April, ~75% of the cost occurs after 22 April (Pekins et al. 1998). Further, because poor maternal condition is related to high neonatal mortality (Verme 1965, 1969, 1977), the combination of high energy demands and low energy reserves means that availability of spring forage is critical to successful reproduction and recruitment in northern deer populations (Pekins et al. 1998).

The condition of deer entering winter (i.e., the amount of stored fat) should influence MF because it determines the amount of energy that can be derived from other body reserves before an animal begins catabolizing MF. Although condition of study animals in November was not directly assessed, number of fetuses was included in the top MF models for all age classes, and breeding date was included in the top models for deer >1 year old (Tables 2.3, 2.4). Although neither parameter was ever significant, deer carrying more fetuses and deer which bred earlier had higher MF. Does in better

condition tend to breed earlier and be more fecund (Verme 1965, 1969, McCullough 1979, Ozoga and Verme 1982), so the inclusion of these parameters in the top models is likely due to the influence of condition at the beginning of winter. Early breeders and deer carrying more fetuses lost fat at a greater rate in South Carolina (Cothran et al. 1987); however, does in that study only lost 6% of their total fat reserves during gestation, making comparisons with northern deer unwarranted. Gestation is energy costly and may influence survival of pregnant does (Moen 1976, Mautz 1978), but deer are able to minimize this effect by delaying fetal development and the associated energy cost (Armstrong 1950, Pekins et al. 1998). The positive influence of early breeding and greater fecundity on MF in this study suggests that reproductive status has little influence on condition of deer during winter, but higher energy costs in spring mean pregnant deer are more susceptible to prolonged winter conditions that delay spring green-up. Does that are in better condition entering winter are more likely to have adequate fat reserves to meet gestation costs in the event of delayed spring green-up. Since these reproductive parameters are indirect measures of physical condition during fall, they likely underestimate the importance of condition at the beginning of winter.

Several factors influence nutritional condition of white-tailed deer during winter in New Hampshire. The length of time deer experience a negative energy balance accounts for most of the loss of energy reserves, but low temperatures and particularly deep snow accelerate the rate of fat loss and are the primary factors responsible for annual variation in nutritional condition and survival. In years of heavy snowfall, overwinter mortality can be substantial in New Hampshire (unpublished data, NHFG), because deep snow negatively affects condition and also increases susceptibility of deer

to other forms of mortality such as predation (e.g., DelGiudice et al. 2002) and motor vehicle collision (O'Gara and Harris 1988). The WSI proved to be a useful predictor of MF, and thus nutritional condition of deer during winter. Because the WSI is easily calculated from readily available weather data, it provides an inexpensive yet valuable index of conditions that negatively affect the deer herd. However, it is critical that managers consider the proportional influence of snow depth and the timing of severe winter conditions when interpreting the WSI. If deep snow persists in April when most deer have depleted their energy reserves and the energy cost of gestation increases exponentially, mortality, malnutrition, and reduced productivity will be more severe than predicted by WSI alone.

CHAPTER III

PRODUCTIVITY, RECRUITMENT, AND PHYSICAL CHARACTERISTICS OF WHITE-TAILED DEER IN NORTHEASTERN NORTH AMERICA

Introduction

White-tailed deer (*Odocoileus virginianus*) in the northeastern United States and eastern Canada are at or near the northern limit of the species range. Populations in this region are limited by severe winter conditions such as deep snow and low temperatures, and deer densities are relatively low as a result (Patterson and Power 2002, Heffelfinger 2012). These densities are typically well below the carrying capacity of summer habitats, but may be near or above the carrying capacity of winter range in many years (Potvin and Huot 1983). This substantial seasonal variation can complicate interpretation of established density relationships and raises doubt about the utility of traditional metrics of population health.

Reliable estimates of demographic parameters are necessary to effectively manage white-tailed deer populations, and biologists rely on relationships between density, physical condition, and productivity and readily available data from harvested deer to inform management decisions. The relationship between physical condition and density is well established (Roseberry and Klimstra 1975, Severinghaus and Moen 1983), and managers often rely on variation in physical parameters such as body weight and antler measurement as indicators of herd health. Researchers have documented changes

in body weight relative to density (Roseberry and Klimstra 1975); however, annual variation in body weight may be confounded by environmental conditions or changes in reproductive rate (Strickland et al. 2008). Yearling buck weight is typically the best predictor of density because deer in this age class allocate much of their energy to growth (Severinghaus and Moen 1983, Keyser et al. 2005b); doe weight is less reliable as does allocate more energy to fat reserves and reproduction and less to growth (Verme and Ozoga 1980). Antler beam diameter (ABD) is strongly correlated with body mass (Roseberry and Klimstra 1975, McCullough 1982) and reproductive rates (Severinghaus and Moen 1983), and is commonly used to indicate population status relative to carrying capacity.

The negative correlation between density and productivity is also well established (Cheatum and Severinghaus 1950, Verme 1969, McCullough 1979, Woolf and Harder 1979, Dusek et al. 1989); however, measures of productivity respond to changes in density more rapidly than physical condition and may be less sensitive to density-independent influences (Keyser et al. 2005a). Because lactation occurs later in the reproductive cycle than ovulation or pregnancy, it may be more indicative of reproductive success. However, lactation is only a binary indicator as it does not provide information on the number of offspring actually recruited. Because older females are less responsive to short-term environmental factors that may cause higher variation in reproductive effort of younger females (Strickland et al. 2008), they are likely more representative of long-term regional conditions and population health (Jones et al. 2010).

These physical condition-density relationships hold true over a wide range of densities and habitat conditions, but it may be difficult to distinguish density dependent

signals from other factors in areas with highly variable environmental conditions (McCullough 1999). Maternal malnutrition during gestation can affect growth and ultimate body size of male offspring (Monteith et al. 2009), and those exposed to severe winters take longer to reach maximum size regardless of population density (Lesage et al. 2001). Therefore, use of yearling weights as an index of density may be confounded in areas with severe winter weather. Additionally, these measures may be unreliable for low density populations on poor sites because most of the density dependent response occurs as the population nears carrying capacity (McCullough 1999, Keyser et al. 2005a).

Recruitment is one of the most important and problematic demographic parameters to estimate. It is the product of the reproductive rate of the population and fawn survival, but both parameters are difficult to measure directly. Although reproductive rates can be estimated from physical condition data (Severinghaus and Moen 1983), fawn survival rates can vary substantially among regions (Linnell et al. 1995) and years (e.g., Long et al. 1998). Fall lactation rates and fawn:doe ratios can provide reasonable indices of recruitment to fall, and are readily obtained from harvested deer. However, the relationship between lactation rate and fawn recruitment is not clear since hunting seasons in this region occur after most fawns have been weaned (Severinghaus and Cheatum 1956, Gauthier and Barrette 1985), and the fawn:doe ratio may be biased by hunter selectivity (Roseberry and Klimstra 1974, Coe et al. 1980).

Lactation rates and harvest fawn:doe ratios declined from the 1980s to 2012 in several northeast jurisdictions. Conversely, body weights and antler measures have remained relatively stable and are indicative of populations in good nutritional condition. This seeming contradiction between stable condition metrics and declining recruitment

indices is of concern to managers. It is possible that antler measures and body weights may not provide sensitive enough indices of density relative to carrying capacity or may be influenced by severe winters. Severe winter conditions such as deep snow and low temperature that cause malnutrition of pregnant deer can result in increased neonatal mortality and reduced productivity (Verme 1963, 1968, 1977, Lavigne 1999). Increased predation on fawns may also be occurring and could provide a simple explanation for decline in recruitment to fall. Populations of black bear (*Ursus americanus*) and eastern coyote (*Canis latrans*) have increased in the northeast since the 1980s (unpublished data; New Hampshire Fish and Game Department [NHFG], Vermont Fish and Wildlife Department [VFWD], Maine Department of Inland Fisheries and Wildlife [MDIFW]), and many studies indicate that these are substantial predators of fawns (e.g., Long et al. 1998, Ballard et al. 1999, Campbell et al. 2005, Carstensen et al. 2009).

Accurately predicting recruitment, and thus population growth rate, is critical for deer population management. In order to make informed decisions it is necessary to understand the relationships among density, physical condition, and productivity in strongly seasonal northern environments, and most importantly, how these factors, winter severity, and fawn survival rate influence recruitment.

This study examined temporal change in reproductive rates as well as physical measures and recruitment indices from harvested deer in northeastern North America. Additionally, predictive relationships among population density, physical condition, winter severity, productivity, and recruitment were evaluated. Improved understanding of these relationships will help biologists and managers make informed management recommendations and provide insight into declining recruitment indices in the region.

Methods

Data Sources

Data for this study were obtained from the states of Vermont, New Hampshire, and Maine, and the Canadian province of New Brunswick; these 4 adjacent jurisdictions are near the northeastern limit of white-tailed deer range (Fig. 3.1). Productivity data based on fetal counts from winter mortalities were obtained from 1999, 2001, 2004, 2008-2009, and 2011-2012 in Vermont, from 1972, 1975-1987, and 2011-2012 in New Hampshire, from 2011-2012 in Maine, and from 2001-2010 in New Brunswick (Appendix D). Data from New Hampshire, Maine, and New Brunswick included pregnancy rate and fecundity (fetuses per pregnant doe) of fawn, yearling, and adult (>2 years old) age classes; Vermont did not differentiate yearlings from older deer, so yearlings and adults were combined for some analyses. Biological data from harvested deer was also obtained; each jurisdiction operated biological check stations annually to collect data which provided indices of physical condition and productivity. Measurements included field-dressed body weights of male and female fawns and yearlings, yearling antler beam diameter (YABD) and points, and yearling and adult lactation rate. Deer age was determined by cementum annuli analysis from an extracted central incisor (Low and Cowan 1963, Gilbert 1966), or the tooth replacement and wear method (Severinghaus 1949). Antler beam diameter was measured 2.5 cm above the pedicle and antler points were >2.5 cm long. Biological data were obtained from New Hampshire from 1974-2012, Vermont from 1995-2012, Maine from 1999-2012, and New Brunswick from 1980-2012; all measurements were not available for all years or jurisdictions (Appendix E).

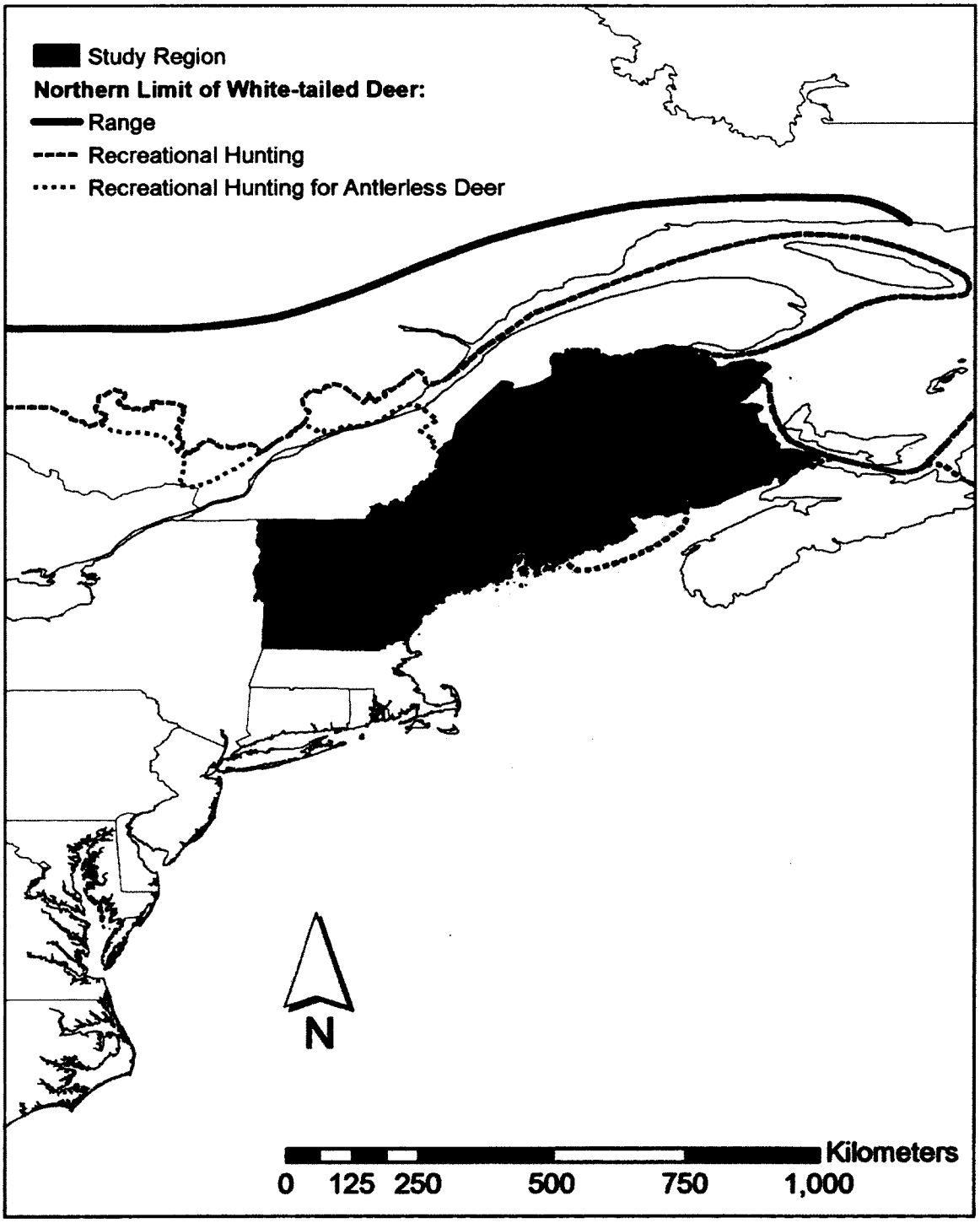

Figure 3.1. Location of the study region near the northern limit of white-tailed deer range. Study region included the states of Vermont (VT), New Hampshire (NH), and Maine (ME), and the Canadian province of New Brunswick (NB). Range limit adapted from Heffelfinger (2012). Limits of recreational hunting developed from 2012 hunting regulations in respective jurisdictions.

Because biological data collection seeks to obtain adequate sample sizes from each age class and region, it may be less representative of the actual distribution of those age classes in the population. Therefore, the total number of adults and fawns of each sex harvested annually in each jurisdiction was used to calculate the ratio of fawns to does >1 year old; this ratio was used as an index of recruitment. Some error was known to occur when distinguishing fawns from older deer at reporting stations not staffed by a biologist, but this should have been consistent over time (K. Gustafson, NHFG, personal communication). Annual adult male harvest density was used as an index of population density. Since antlerless deer harvests in this region are influenced primarily by management decisions (e.g., number of permits issued), antlered buck harvest provides the best objective metric of relative population density in each jurisdiction over time.

Winter severity index (WSI) data were also obtained from each jurisdiction. New Hampshire and Vermont used the same WSI which summed the number of days with snow depth ≥46 cm (18 in) and the number of days with minimum temperature ≤-18 °C (0 °F) between 1 December and 30 April. Maine's WSI incorporated a measure of deer sinking depth while New Brunswick's only included snow depth; the data were standardized by jurisdiction ($[x-\bar{x}]/\sigma$) to account for these differences. Since the relationship between WSI and actual winter mortality may vary among jurisdictions and WSI is typically used as a relative index, standardization should not affect the utility of these data.

Statistical Analyses

Temporal Trends

Biological and harvest data from all 4 jurisdictions were analyzed to assess temporal change in the physical condition and productivity of the deer populations. Data were divided into 5 roughly equal time periods (1987-1991, 1992-1996, 1997-2001, 2002-2006, and 2007-2012) and analyzed by jurisdiction. Productivity data from Vermont and New Brunswick were analyzed using the same time periods; New Hampshire data were compared between 1980-1987 and 2011-2012. Summary productivity data from Maine for the period 1980-1989 are presented, but did not allow for meaningful statistical comparison to data from 2011-2012. Analysis of variance (ANOVA) was used to test for differences among time periods in physical parameters and productivity indices. Pairwise comparisons were made with Tukey's test and significance level was set *a priori* at $\alpha = 0.05$ for all tests.

Model Development

The utility of physical parameters, population density, and winter severity as predictors of productivity and recruitment (i.e., harvest fawn:doe ratio) was explored using generalized linear mixed regression models (GLMM) using the *lme4* package (Bates et al. 2012) in R (R Development Core Team 2011). Model parameters included YABD, yearling male weight, fawn recruitment, WSI, and population density (buck harvest density) for each jurisdiction; all data were standardized ($[x-\bar{x}]/\sigma$) and year and jurisdiction were included as random effects in all models (Table 3.1). Thirty-two competing models were developed to explain pregnancy rates of fawns and deer >1 year old and fecundity of deer >1 year old; sufficient data were not available to develop a

Table 3.1. Variables used in generalized linear mixed effects models to explain productivity and recruitment of white-tailed deer in 4 northeastern jurisdictions.

Explanatory Variable	Effect	Parameters	Type
Year	Random	1970-2012	Categorical
Jurisdiction	Random	ME, NB, NH, VT	Categorical
Yearling antler beam diameter	Fixed	-2.80-2.50[3]	Numerical
Yearling male weight	Fixed	-2.00-2.60[3]	Numerical
Fawn recruitment[1]	Fixed	-1.93-2.25[3]	Numerical
Winter severity	Fixed	-1.67-3.42[3]	Numerical
Population Density	Fixed	-1.63-2.78[3]	Numerical
1+ fecundity[2]	Fixed	-1.88-1.89[3]	Numerical

[1] Only included in productivity models

[2] Only included in recruitment models

[3] Data were standardized; values represent standard deviations from the mean

reliable model for fawn fecundity. Similarly, 32 competing models were developed to explain recruitment; fecundity of deer >1 year old was also included as a parameter in recruitment models. The best fitting models were determined by using the lowest second-order Akaike Information Criterion (AIC_c) scores with the *AICcmodavg* package (Mazerolle 2012) in R. Models with shared AIC_c weight and ΔAIC_c scores <2 were averaged using the *MuMIn* package (Barton 2013) in R; model averaging can lead to more precise parameter estimates (Burnham and Anderson 2002, Bolker et al. 2008).

Results

Trends in Productivity, Recruitment, and Physical Condition

There were no differences (P >0.05) among time periods in pregnancy rate or fecundity of adults, or yearlings and adults combined in any jurisdiction. Yearling pregnancy was also not different among time periods in any jurisdiction, although it declined 21% in New Brunswick from 1996-2001 to 2007-2012 (P = 0.075) and 35% in Maine from the 1980s to 2011. Yearling fecundity declined 21% in New Brunswick from 1996-2001 to 2007-2012 (P = 0.029) and 20% in Maine from the 1980s to 2011; there were no differences among time periods in New Hampshire. Fawn fecundity was not different among time periods in any jurisdiction, but fawn pregnancy rate declined 79% in New Brunswick (P = 0.030) and 100% in Vermont (P = 0.001) from 1996-2001 to 2007-2012. In New Hampshire, fawn pregnancy rate declined 78% from 1980-1987 to 2011-2012 (P = 0.055). In Maine, fawn pregnancy rate was 0.39 during 1980-1989 and 0.05 during 2011-2012 (Fig 3.2).

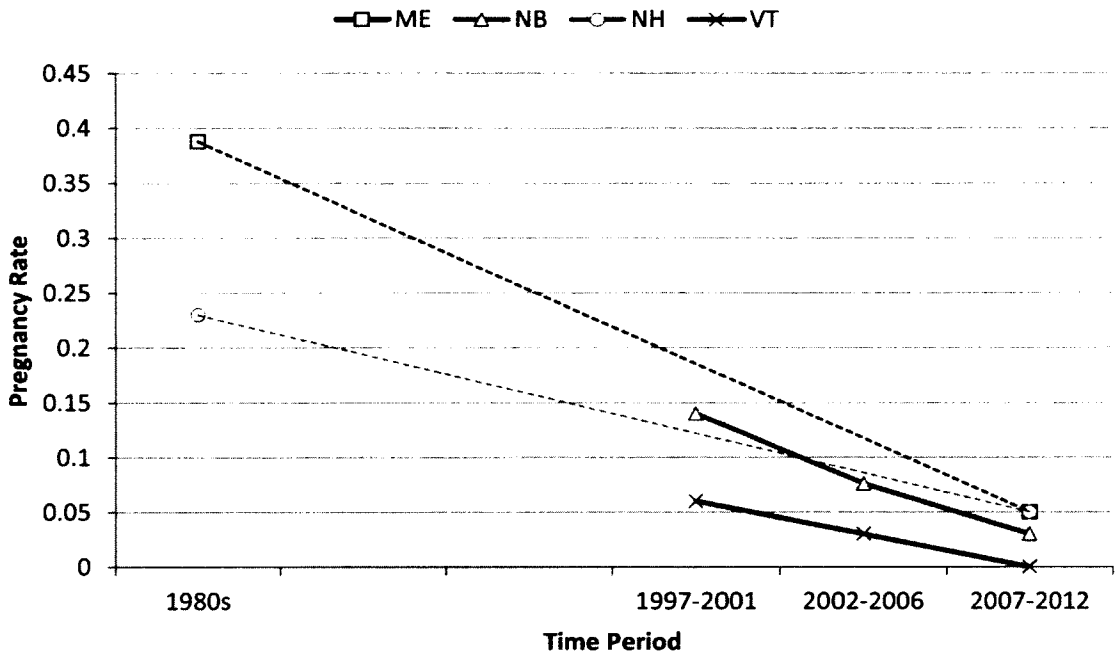

Figure 3.2. Temporal trends in fawn pregnancy rates in Maine, New Brunswick, New Hampshire, and Vermont from the 1980s through 2012. Pregnancy rate decreased in all jurisdictions ($P < 0.05$)

There were no differences (P >0.05) among time periods in any jurisdiction for YABD, yearling antler points, yearling doe weight, or fawn weights. Yearling buck weight increased 3.0 kg (6%; P = 0.004) in Vermont and 4.9 kg (9%; P <0.001) in New Brunswick from 1992-1996 to 2007-2012; there were no differences among time periods in New Hampshire or Maine (Fig. 3.3).

The harvest fawn:doe ratio declined 53% in Vermont (P <0.001) and 71% in New Brunswick (P <0.001) from 1987-1991 to 2007-2012. In New Hampshire, the fawn:doe ratio peaked during 1992-1996 and declined 36% to 2007-2012 (P <0.001). In Maine, the fawn:doe ratio was highest during 1997-2001 and 2002-2006 and declined 12% from 2002-2006 to 2007-2012 (P = 0.024; Fig. 3.4).

Adult and yearling lactation rates decreased 16% (P = 0.020) and 68% (P = 0.003), respectively, from 1992-1996 to 2007-2012 in New Hampshire. Lactation rates were not different among the 3 time periods for which data were obtained from New Brunswick (1997-2001 to 2007-2012); similarly, there were no differences among those 3 time periods in New Hampshire (Fig 3.5).

The mean annual antlered buck harvest increased consistently in New Hampshire and was 62% higher in 2007-2012 than in 1987-1991 (P <0.001). In New Brunswick, buck harvest declined 41% from 1987-1991 to 1997-2001 (P = 0.008) and remained relatively stable thereafter. Buck harvest in Maine peaked in 1997-2001 and declined 29% to 2007-2012 (P <0.001). Similarly, Vermont's buck harvest peaked in 1992-1996 and 1997-2001 and declined 35% to 2002-2006 (P = 0.002; Fig. 3.6).

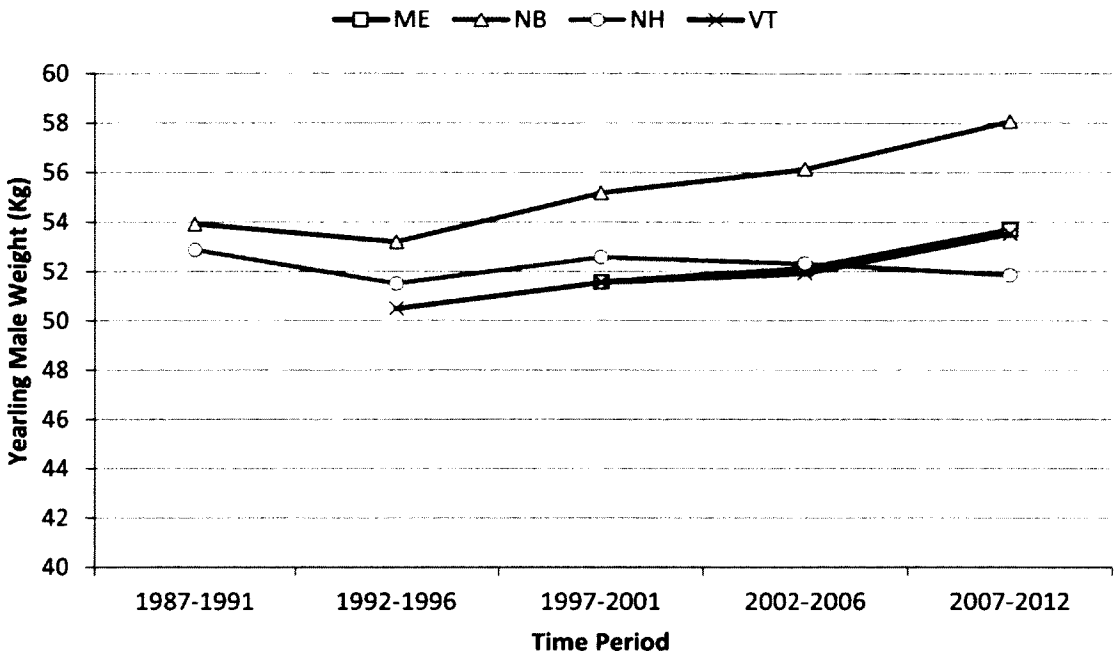

Figure 3.3. Temporal trends in field-dressed body weight of yearling bucks examined at biological check stations in Maine, New Brunswick, New Hampshire, and Vermont, 1987-2012. Maine data are from 1999-2012 and Vermont data are from 1995-2012. Weights increased in New Brunswick and Vermont from 1992-1996 to 2007-2012 ($P < 0.05$).

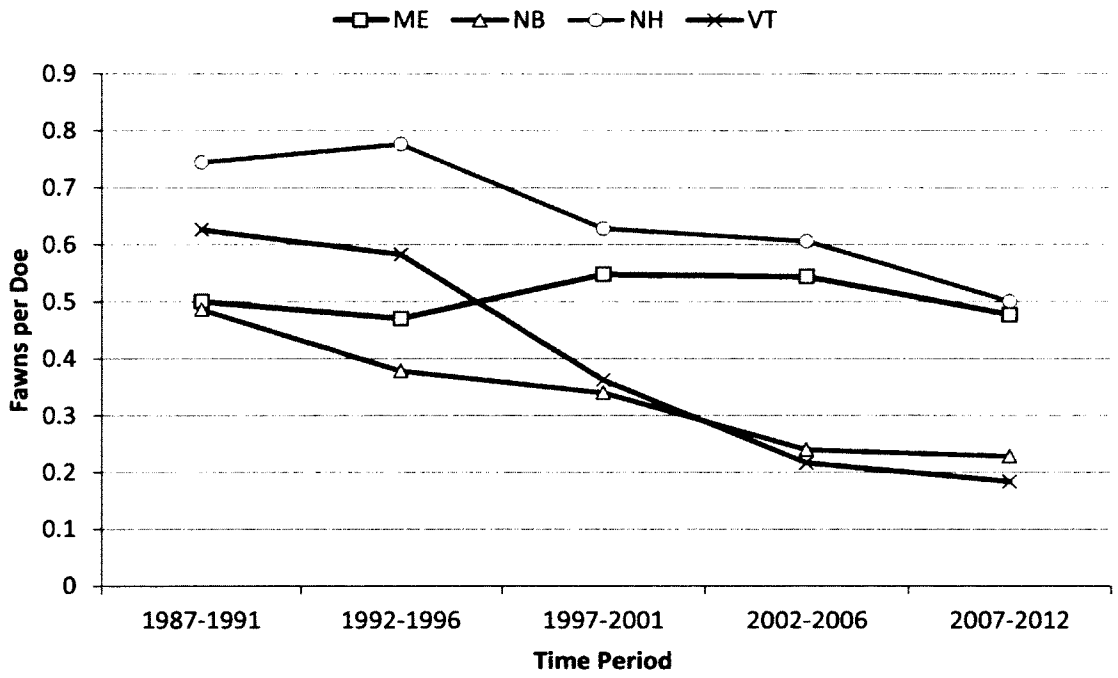

Figure 3.4. Temporal trends in the ratio of fawns to does >1 year old in the harvest in Maine, New Brunswick, New Hampshire, and Vermont, 1987-2012. Long-term declines are evident in all jurisdictions except Maine. Differences among jurisdictions are likely related to season structure and hunter selectivity rather than actual differences in fawn recruitment.

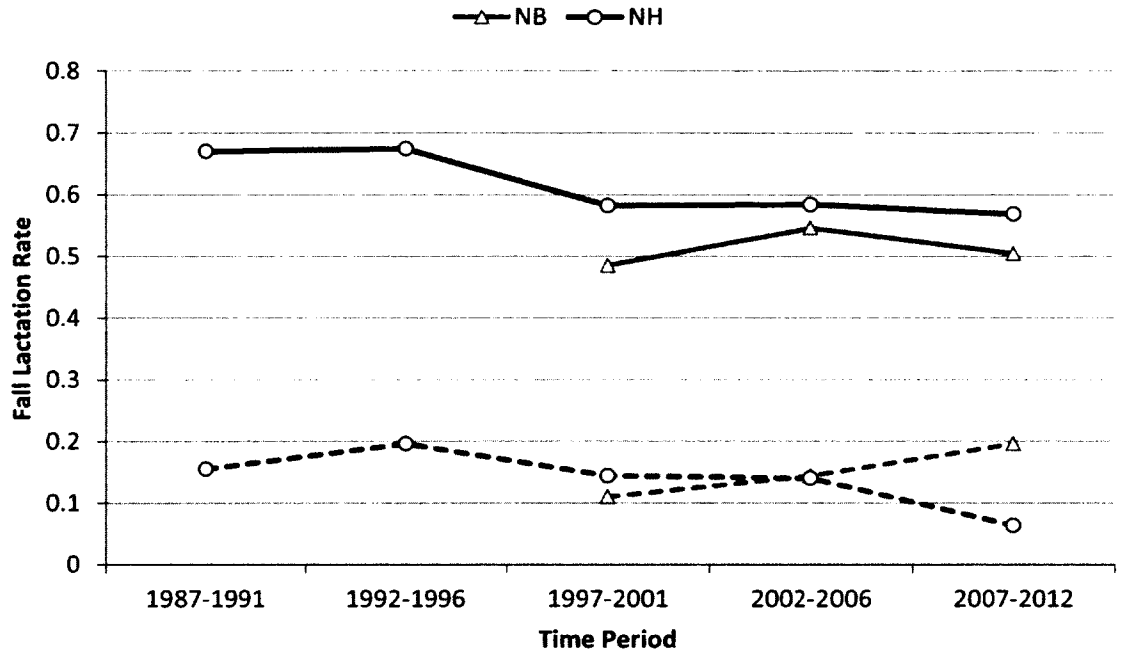

Figure 3.5. Temporal trends in lactation rates of yearling (dashed lines) and adult (>2 years old; solid lines) does examined at biological check stations in New Brunswick and New Hampshire, 1987-2012. New Brunswick data are from 2000-2012. Lactation rate declined in both age classes in New Hampshire ($P < 0.05$), but was not different among time periods in New Brunswick.

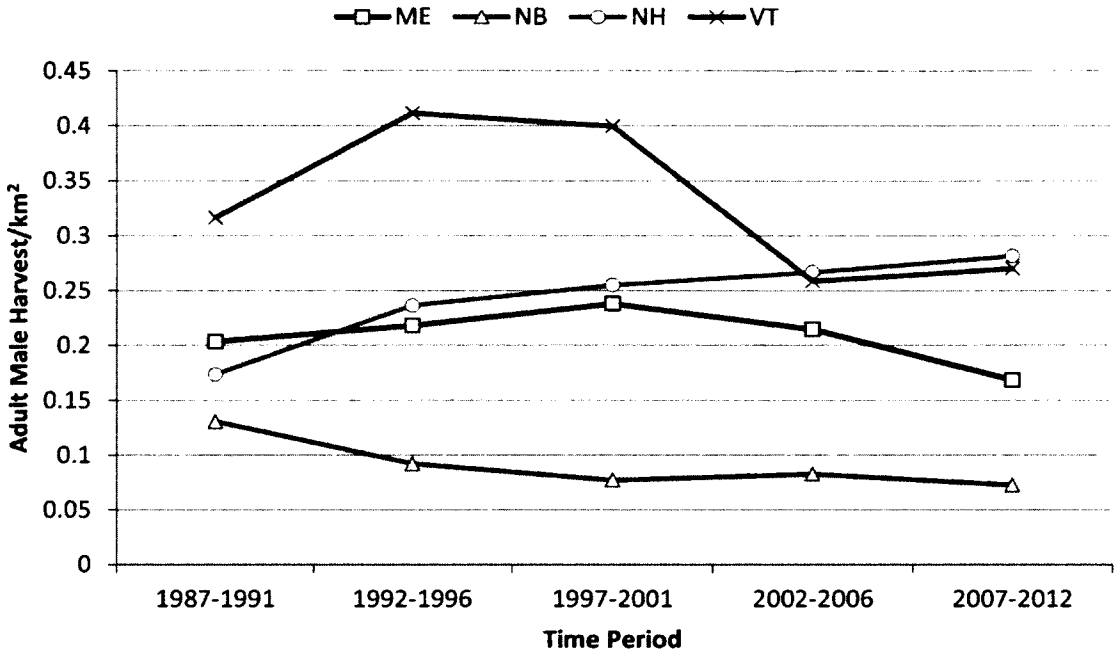

Figure 3.6. Temporal trends in white-tailed deer population density (i.e., adult male harvest density) in Maine, New Brunswick, New Hampshire, and Vermont, 1987-2012.

Recruitment and Productivity Models

Thirty-two competing models were tested to explain annual differences in observed fawn recruitment; the parameters of the 2 top models were averaged to explain recruitment (Table 3.2). The highest recruitment was observed during times of lower density, lower YABD, and lower WSI (Table 3.2).

Thirty-two competing models were tested to explain age-specific pregnancy and fecundity rates. Fawn pregnancy rate was highest following less severe winters and was positively related to YABD (Table 3.3). The top model for pregnancy of deer >1 year old indicated pregnancy was positively related to YABD, recruitment, and density (Table 3.4). Fecundity of deer >1 year old was positively related to yearling buck weight, recruitment, and density (Table 3.5).

Discussion

Physical Condition and Productivity

The observed increase in yearling male weight in New Brunswick and Vermont was concurrent with decline in density, which is consistent with previous research (Severinghaus and Moen 1983, Keysar et al. 2005b). Temporal differences in Maine, where the population declined substantially after the 1997-2001 time period, were nearly identical to Vermont (Fig. 3.2); a lack of weight data from earlier time periods in Maine limited statistical inference. Given dissimilar temporal patterns of density, the parallel nature of the increases in Vermont, Maine, and New Brunswick seemingly implicate additional, exogenous factors. Similarly, a decline in yearling male weight might have been expected in New Hampshire given its substantial increase in density.

Table 3.2. Comparison of 32 recruitment models developed from productivity, physical condition, density, and winter severity (WSI) data from Maine, New Brunswick, New Hampshire, and Vermont. Parameter estimates for top models (ΔAIC_c <2) were averaged using the *MuMIn* package in R.

Model	K	AIC_c	ΔAIC_c	w_i	LL
Density, YABD, fecundity	7	17.8	0.0	0.53	1.39
YABD, WSI, fecundity	7	18.3	0.5	0.41	1.13
Density, YABD, WSI, fecundity	8	22.3	4.5	0.06	1.35
Density, YBWT, fecundity	7	37.7	19.9	0.00	-8.55
Density, YABD, YBWT, fecundity	8	40.2	22.4	0.00	-7.61
YBWT, fecundity	6	41.4	23.6	0.00	-12.36
YABD, YBWT, fecundity	7	41.8	24.0	0.00	-10.62
Density, YBWT, WSI, fecundity	8	42.1	24.3	0.00	-8.54
Density, YABD, YBWT, WSI, fecundity	9	44.3	26.5	0.00	-7.17
YBWT, WSI, fecundity	7	45.2	27.4	0.00	-12.31
YABD, fecundity	6	45.9	28.0	0.00	-14.59
YABD, YBWT, WSI, fecundity	8	46.2	28.4	0.00	-10.60
Density, WSI, fecundity	7	48.1	30.3	0.00	-14.80
Density, fecundity	6	53.3	35.5	0.00	-19.02
fecundity	5	68.9	51.1	0.00	-28.36
WSI, fecundity	6	70.9	53.1	0.00	-27.85
Density, YBWT, WSI	7	101.4	83.6	0.00	-42.92
YBWT, WSI	6	101.9	84.1	0.00	-44.38
Density, YABD, YBWT, WSI	8	102.7	84.9	0.00	-42.33
YABD, YBWT, WSI	7	103.2	85.4	0.00	-43.81
YBWT	5	142.9	125.1	0.00	-66.10
Density, YBWT	6	144.0	126.2	0.00	-65.49
YABD, YBWT	6	145.2	127.4	0.00	-66.07
Density, YABD, YBWT	7	146.3	128.5	0.00	-65.45
Density, YABD, WSI	7	152.8	135.0	0.00	-68.83
YABD, WSI	6	154.4	136.6	0.00	-70.80
Density, YABD	6	217.0	199.2	0.00	-102.13
YABD	5	218.0	200.2	0.00	-103.73
WSI	5	284.0	266.2	0.00	-136.77
Density, WSI,	6	285.1	267.3	0.00	-136.23
Intercept only	4	318.0	300.2	0.00	-154.87
Density,	5	318.6	300.8	0.00	-154.08

Model-averaged coefficients:	Estimate	SE	z	Pr(>|z|)
(Intercept)	-0.645	0.542	1.190	0.234
Density	-0.328	0.098	3.343	0.001
YABD	-0.157	0.073	2.150	0.032
Fecundity	0.085	0.086	0.995	0.320
WSI	-0.118	0.003	44.315	<0.001

Table 3.3. Comparison of 32 models of fawn pregnancy rate developed from data from Maine, New Brunswick, New Hampshire, and Vermont. Parameter estimates for top models (ΔAIC_c <2) were averaged using the *MuMIn* package in R. Winter severity and YABD were indicated as important factors in the top models.

Model	K	AIC_c	ΔAIC_c	w_i	LL
YABD	5	42.6	0.0	0.29	-14.71
WSI, YABD	6	43.1	0.6	0.22	-13.23
Recruit, YABD	6	44.8	2.2	0.10	-13.94
Density, YABD	6	45.7	3.1	0.06	-14.52
Recruit, WSI, YABD	7	45.7	3.2	0.06	-12.37
YABD, YBWT	6	45.8	3.2	0.06	-14.56
WSI, YABD, YBWT	7	45.9	3.3	0.06	-12.65
Density, WSI, YABD	7	47.0	4.4	0.03	-13.20
YBWT	5	48.1	5.5	0.02	-17.45
Recruit, Density, YABD	7	48.3	5.8	0.02	-13.66
Recruit, YBWT	6	48.5	5.9	0.02	-15.77
Recruit, YABD, YBWT	7	48.7	6.2	0.01	-13.87
WSI, YBWT	6	49.0	6.4	0.01	-16.16
Density, YABD, YBWT	7	49.4	6.8	0.01	-14.40
Recruit, Density, WSI, YABD	8	50.2	7.6	0.01	-12.30
Recruit, WSI, YABD, YBWT	8	50.3	7.7	0.01	-12.34
Density, WSI, YABD, YBWT	8	50.3	7.7	0.01	-12.64
Recruit, WSI, YBWT	7	50.9	8.4	0.00	-14.97
Density, YBWT	6	51.3	8.7	0.00	-17.29
Density, WSI, YBWT	7	52.0	9.4	0.00	-15.70
Recruit, Density, YBWT	7	52.3	9.7	0.00	-15.63
Recruit, Density, YABD, YBWT	8	52.3	9.8	0.00	-13.38
Recruit, Density, WSI, YABD, YBWT	9	55.5	12.9	0.00	-12.30
Recruit, Density, WSI, YBWT	8	55.5	12.9	0.00	-14.96
Recruit	5	87.3	44.7	0.00	-37.53
Recruit, WSI	6	88.4	45.8	0.00	-36.58
Recruit, Density	6	89.4	46.9	0.00	-37.10
Recruit, Density, WSI	7	91.0	48.4	0.00	-36.27
Density	5	96.2	53.7	0.00	-42.05
Intercept only	4	96.3	53.8	0.00	-43.48
Density, WSI	6	97.7	55.1	0.00	-41.29
WSI	5	98.2	55.6	0.00	-43.03

Model-averaged coefficients:	Estimate	SE	z	Pr(>|z|)
(Intercept)	-0.401	0.104	3.856	<0.001
YABD	0.185	0.064	2.901	0.004
WSI	-0.172	0.102	1.692	0.091

Table 3.4. Comparison of 32 models for pregnancy rate of deer >1 year old developed from data from Maine, New Brunswick, New Hampshire, and Vermont. Density, WSI, and YABD were indicated as important factors in the top model.

Model	K	AIC_c	ΔAIC_c	w_i	LL
Recruitment, Density, YABD,	7	71.2	0.0	0.50	-25.32
Density, YABD,	6	74.3	3.1	0.11	-28.96
Recruitment, Density, WSI, YABD,	8	74.4	3.2	0.10	-24.69
Recruitment, Density, YBWT	7	75.0	3.8	0.08	-27.20
Recruitment, Density, YABD, YBWT	8	75.2	4.0	0.07	-25.09
Density, YABD, YBWT	7	76.8	5.6	0.03	-28.30
Recruitment, Density, WSI, YBWT	8	76.9	5.7	0.03	-25.95
Density, WSI, YABD,	7	77.3	6.0	0.02	-28.52
Recruitment, Density, WSI, YABD, YBWT	9	77.4	6.2	0.02	-23.70
Density, YBWT	6	77.9	6.7	0.02	-30.72
YABD,	5	80.2	9.0	0.01	-33.59
Recruitment, YABD,	6	80.6	9.4	0.01	-31.96
Density, WSI, YABD, YBWT	8	80.9	9.7	0.00	-28.22
Density, WSI, YBWT	7	81.6	10.4	0.00	-30.68
YABD, YBWT	6	83.1	11.9	0.00	-33.33
YBWT	5	83.4	12.2	0.00	-35.20
WSI, YABD,	6	83.6	12.4	0.00	-33.58
Recruitment, YABD, YBWT	7	83.7	12.5	0.00	-31.56
Recruitment, YBWT	6	84.2	13.0	0.00	-33.77
Recruitment, WSI, YABD,	7	84.5	13.3	0.00	-31.95
WSI, YBWT	6	86.8	15.6	0.00	-35.20
WSI, YABD, YBWT	7	86.8	15.6	0.00	-33.31
Recruitment, WSI, YABD, YBWT	8	87.7	16.5	0.00	-31.35
Recruitment, WSI, YBWT	7	88.1	16.9	0.00	-33.75
Recruitment, Density,	6	92.6	21.4	0.00	-38.76
Recruitment, Density, WSI,	7	95.7	24.5	0.00	-38.72
Density,	5	100.0	28.7	0.00	-43.94
Recruitment,	5	101.4	30.2	0.00	-44.65
Density, WSI,	6	102.7	31.5	0.00	-43.85
Intercept only	4	103.1	31.9	0.00	-46.90
Recruitment, WSI,	6	104.0	32.8	0.00	-44.43
WSI,	5	105.1	33.9	0.00	-46.51

Model coefficients:	Estimate	SE	z	Pr(>|z|)
(Intercept)	0.405	0.220	1.844	0.079
YABD	0.326	0.143	2.273	0.034
Recruitment	0.401	0.146	2.754	0.012
Density	0.357	0.156	2.293	0.032

Table 3.5. Comparison of 32 models for fecundity of deer >1 year old developed from data from Maine, New Brunswick, New Hampshire, and Vermont. Density, recruitment rate, and yearling male weight were indicated as important factors in the top model.

Model	K	AIC_c	ΔAIC_c	w_i	LL
Recruitment, Density, YBWT	7	72.1	0.0	0.53	-25.77
Recruitment, Density, YABD, YBWT	8	75.6	3.4	0.10	-25.28
Recruitment, Density, WSI, YBWT	8	75.7	3.6	0.09	-25.35
Density, WSI, YABD,	7	77.1	4.9	0.05	-28.42
Recruitment, Density, WSI, YABD,	8	77.7	5.6	0.03	-26.35
Recruitment, Density, YABD,	7	78.1	5.9	0.03	-28.73
Recruitment, WSI, YABD,	7	78.2	6.1	0.03	-28.81
Recruitment, YBWT	6	78.3	6.2	0.02	-30.83
Recruitment, WSI, YBWT	7	78.5	6.4	0.02	-28.96
Recruitment, YABD,	6	78.9	6.8	0.02	-31.12
WSI, YBWT	6	79.2	7.0	0.02	-31.37
Recruitment, Density, WSI, YABD, YBWT	9	79.3	7.2	0.01	-24.66
WSI, YABD,	6	79.7	7.6	0.01	-31.64
YABD,	5	79.9	7.8	0.01	-33.47
YBWT	5	80.0	7.8	0.01	-33.48
Density, YABD,	6	80.9	8.8	0.01	-32.25
Density, YBWT	6	81.1	9.0	0.01	-32.35
Density, WSI, YABD, YBWT	8	81.3	9.1	0.01	-28.39
WSI, YABD, YBWT	7	81.8	9.7	0.00	-30.81
Recruitment, YABD, YBWT	7	82.2	10.1	0.00	-30.83
Recruitment, WSI, YABD, YBWT	8	82.6	10.5	0.00	-28.81
YABD, YBWT	6	83.0	10.9	0.00	-33.29
Density, WSI, YBWT	7	83.0	10.9	0.00	-31.39
Density, YABD, YBWT	7	84.3	12.2	0.00	-32.03
Recruitment, WSI,	6	101.4	29.3	0.00	-43.11
WSI,	5	102.6	30.5	0.00	-45.22
Recruitment,	5	103.1	31.0	0.00	-45.44
Recruitment, Density, WSI,	7	104.7	32.6	0.00	-43.12
Recruitment, Density,	6	104.8	32.7	0.00	-44.77
Intercept only	4	104.8	32.7	0.00	-47.73
Density, WSI,	6	106.1	33.9	0.00	-45.48
Density,	5	106.2	34.0	0.00	-47.01

Model coefficients:	**Estimate**	**SE**	**z**	**Pr(>|z|)**
(Intercept)	0.676	0.217	3.119	0.005
Recruitment	0.894	0.187	4.791	<0.001
Density	0.595	0.162	3.677	0.001
YBWT	0.682	0.176	3.870	<0.001

The lack of difference among time periods in the other physical parameters also suggests minimal influence of density on the physical condition of deer in these populations. This is not surprising considering the relatively low density of each population (~3-6 deer/km^2; unpublished data, VTFW, NHFG, MDIFW, New Brunswick Department of Natural Resources [NBDNR]). Physical measures may be unreliable for low density populations because most density-dependent response occurs as a population nears carrying capacity (McCullough 1999). Additionally, any effect of low density on physical parameters is likely confounded or completely masked by environmental factors (e.g., winter weather, mast crops). Patterson and Power (2002) similarly noted that YABD did not decrease as density increased during the 1990s in Nova Scotia, which they suggested was due to a time lag in deer density and the quality or quantity of available forage. No evidence of a time lag was detected in this study, as YABD did not change in any jurisdiction during the 26 year study period despite substantial changes in deer densities. The YABD in all 4 jurisdictions in this study and in Nova Scotia was consistently >16 mm, indicating healthy populations that were presumably below ecological carrying capacity (K, *sensu* McCullough 1979)

Although these deer populations are well below the carrying capacity of summer habitat, they may be near or above the carrying capacity of winter range in many years. Winter K can vary annually due to variation in WSI, particularly deep snow which reduces forage availability and confines deer to smaller portions of their range (Potvin and Huot 1983). Minimal intraspecific competition during spring, summer, and fall may allow many deer to fully recover; therefore, early evidence of density-dependence may be

associated with WSI rather than absolute density or physical condition during October-November.

There were no differences among time periods and no apparent trend in WSI, but 6 of the 10 most severe winters in Maine occurred from 2001-2011, including the top 3 (unpublished data, MDIFW). The relative condition and availability of DWAs have declined throughout much of the region due in large part to a widespread spruce budworm (*Choristoneura fumiferana*) outbreak and large scale, salvage timber harvests in the 1980s (Lavigne 1999). Increased competition for limited winter forage could cause reduced nutritional condition in spring and result in higher neonatal mortality and reduced productivity (Verme 1963, 1965, 1977).

Fecundity and pregnancy rate of deer >1 year old remained stable over the study period, despite changes in density. Models for both pregnancy and fecundity identify density as an important factor, but the relationship is positive which probably reflects the use of buck harvest as a density index. Environmental conditions or other factors which promote higher pregnancy and fecundity would presumably promote greater adult survival and thus higher buck harvest, explaining the positive relationship. The positive relationships between fecundity and yearling buck weight, and pregnancy and YABD are consistent with previous research (Severinghaus and Moen 1983) and reinforce the validity of these metrics as predictors of productivity even at relatively low population density. Without any substantial density-dependence at play in these populations, it is likely that exogenous factors which promote larger YABD and greater yearling buck weights also permit females to be in better physical condition and more fecund, and explain the positive relationship between the recruitment rate and subsequent

productivity. Some researchers have found an inverse relationship between fecundity and prior reproductive success, suggesting that does that lose fawns during gestation or shortly after birth recover more quickly to top physical condition and are subsequently more fecund (Verme 1967, Mansell 1974). While possible for individual deer, it is unlikely to be the case for the populations in this study.

Fawn pregnancy rates are usually minimal in areas with severe winters (Severinghaus and Cheatum 1956, Ozoga and Verme 1982, Dusek et al. 1989, Campbell et al. 2005, DelGiudice et al. 2007), but were relatively high in Maine and New Hampshire during the 1980s (39% and 23%, respectively). The fawn pregnancy rate was consistent across the region, with all jurisdictions ≤5% during 2007-2012. However, it is not clear how fawn pregnancy rate may have changed during the period between the 1980s and 2011 in Maine and New Hampshire, or what it was prior to 1999 and 2001 in Vermont and New Brunswick, respectively. The positive relationship with YABD, similar to that with pregnancy of older deer, suggests this widely used metric is a useful predictor of productivity. The negative relationship with winter severity is also consistent with previous research; severe winter conditions that result in malnourishment of pregnant does reduces birth weight (Verme 1963, 1965, 1977) and growth during the nursing period (Therrien et al. 2008). As a result, severe winters limit the number of individuals able to reach critical mass and condition thresholds for puberty prior to onset of winter weather. Although WSI showed no consistent trend in any jurisdiction, greater frequency of severe winters since 2001 in combination with reduced availability of DWAs could have functionally increased the impact of WSI.

Similar declines in yearling pregnancy and fecundity in Maine and New Brunswick indicate a clear reduction in productivity of younger age classes. However, the lack of decline in yearling productivity in New Hampshire confounds the argument that severe winter weather or lack of DWAs were highly influential throughout the region. Widespread access to supplemental food can disproportionately improve the nutritional status of wintering fawns (Tarr and Pekins 2002) and therefore increase yearling reproductive rates (Ozoga and Verme 1982), but supplemental feeding was not limited to New Hampshire. Unfortunately, limited data availability did not facilitate modeling of yearling productivity measures.

Physical condition and productivity of these populations were not directly influenced by density; however, density-dependence may manifest differently in areas with substantial seasonal variation in K. Despite this variation, YABD and yearling buck weight were meaningful predictors of productivity, confirming the validity of these widely used metrics even in strongly seasonal northern environments. Within the relatively low and narrow range of densities found in these populations, annual variation in exogenous environmental factors, including WSI, is likely the primary cause of change in physical condition and productivity. Management agencies should continue to directly monitor productivity to provide better long-term datasets and elucidate relationships with environmental variables. Continued monitoring of WSI, in concert with accurate and updated mapping of DWAs, and knowledge of the quantity and extent of supplemental feeding will provide insight into winter K and its potential impact on productivity of younger age classes.

Recruitment

The weak relationship between fecundity of deer >1 year old and recruitment is surprising; however, the sparse availability of productivity data may have limited detection of relationships. Nonetheless, recruitment declined substantially in 3 of the 4 jurisdictions from 1987-1991 to 2007-2012 where productivity of adult deer remained unchanged, suggesting that decline in recruitment was related to other factors. Decline in yearling pregnancy and fecundity, as observed in Maine and New Brunswick, could cause reduced recruitment, but this would not explain the substantial decline in New Hampshire where yearling pregnancy and fecundity were unchanged. The observed decline in fawn pregnancy rate would also not account for decline in recruitment. Although fawns may account for up to 30% of the female population, a reduction in fawn pregnancy rate from 30% to 5% would only result in a 7% decline in total fawn production as long as productivity of older deer remained constant. Additionally, offspring of primiparous mothers have lower survival rates than those of older does (Verme 1969, Ozoga and Verme 1986a, b, Dusek et al. 1989), making it unlikely that productivity by fawns has ever had a substantial impact on recruitment in this region. In fact, expected recruitment based on age-specific birth rates actually increased in New Hampshire from the 1980s to 2011-2013, primarily due to a higher proportion of older deer in the population (see Chapter 1).

Density, WSI, and YABD were negatively related to recruitment in the top model. Declining recruitment might be expected as population density increases, but recruitment declined steadily from 1987-1991 to 2007-2012 in Vermont, New Hampshire, and New Brunswick despite differing trends in density (Figs. 3.4 and 3.6). Similarly, severe winter

conditions are expected to reduce recruitment due to increased neonatal mortality (Verme 1977, Sams et al. 1996). Although WSIs were relatively stable over time in each jurisdiction, it is possible that reduced quality and quantity of DWAs has functionally increased the impact of WSI. Because WSI affects winter K and these populations are only near K during winter, WSI and density are closely related. Therefore, it is likely that winter severity affects annual variation in recruitment, but given the steady nature of the declines, other factors were probably responsible for much of the observed change during the study period. The negative relationship between YABD and recruitment is counterintuitive and similarly suggests that the decline in recruitment was caused, at least in part, by factors not included in the model.

One possible explanation for the decline in recruitment is that predation of fawns may have increased. Populations of black bear and eastern coyote have increased throughout the region since the 1980s (unpublished data, NHFG; VFWD; MDIFW; NBDNR), and many studies indicate they are substantial predators of fawns (e.g., Long et al. 1998, Ballard et al. 1999, Patterson et al. 2002, Campbell et al. 2005, Carstensen et al. 2009). Higher fawn predation provides a simple explanation for the consistent declines in recruitment and the lack of any apparent relationship to productivity. However, the lack of a consistent recruitment decline in Maine would seem to negate predation as the sole factor, since predator densities were not substantially different among jurisdictions.

Management decisions may also influence recruitment rates. Unlike much of the white-tailed deer's range (where reducing overabundant populations is a primary management goal), management in these populations was generally focused on increasing deer numbers by reducing harvest of antlerless deer. Although the methods of

reducing antlerless harvest varied among jurisdictions, the result was greater survival rates for female deer. With more adult does available, some hunters may have become less likely to harvest fawns (Coe et al. 1980). If so, it could partially account for much of the observed decline in both fawn:doe ratio and lactation rates, and the consistent, steady nature of the declines. The potential influence of hunter selectivity on the harvest fawn:doe ratio was most obvious in Vermont because New Hampshire, Maine, and New Brunswick had either-sex hunting seasons (i.e., no restriction on antlerless harvest) until the 1980s. Years of male-biased harvest in Vermont likely reduced the proportion of antlered bucks in the population, and many hunters may avoid harvesting fawns to enhance the probability of male fawn survival. A clear illustration of this is the discrepancy in fawn:doe ratios between Vermont's general antlerless harvest (0.18 fawns per doe in 2007-2012) and their youth weekend antlerless harvest (0.54). Since it is unlikely that youth hunters exhibit substantial selectivity during such a short season, this ratio was probably more representative of the actual population recruitment rate, and was very similar to ratios observed in New Hampshire (0.50) and Maine (0.48) during that time period; youth season data from Vermont were not used in this study because the season was not held prior to 1997. It is not clear what role hunter selectivity may play in the relatively low recruitment rates observed in New Brunswick, but the potential for biased data exists.

Deer populations in all 4 jurisdictions exhibited productivity and physical metrics indicative of populations with high nutritional condition, but recruitment (based on harvest fawn:doe ratio and fall lactation rates) declined steadily in Vermont, New Hampshire, and New Brunswick and during the most recent time periods in Maine.

Multiple factors are likely responsible for declining recruitment including 1) reduced winter K that causes malnutrition and reduced productivity, 2) direct predation of fawns by higher predator populations, and 3) gradual change in hunter selectivity. Substantial decline in recruitment limits the potential population growth rate and is therefore of great consequence to management of deer populations, particularly where winter has strong density-independent influence.

Successful management of these populations will require accurate measures of fawn recruitment and better understanding of the factors influencing summer fawn mortality. Traditional physical condition metrics from harvested deer are useful predictors of productivity, but have little or no value in predicting recruitment. Because decline in physical condition would still be expected if the populations ever approach summer K, or substantially exceed winter K, and these data are easily obtained from harvested deer, continued monitoring is warranted. Continued direct monitoring of productivity should provide the long-term datasets and larger sample sizes necessary to detect relationships between productivity and recruitment, but field studies may be necessary to identify rate and cause of summer fawn mortality. If recruitment indices from harvested deer (i.e., lactation rate, fawn:doe ratio) are to be used, surveys of hunter attitudes toward harvest of fawns and other antlerless deer will provide a better understanding of the potential influence of hunter selection. Reduced nutritional condition resulting from increased density on winter range, or reduced winter K, could account for the simultaneous declines in recruitment and productivity of younger age classes. Accurate and updated mapping of DWAs and estimates of winter K will provide valuable insight into the factors limiting these populations.

CONCLUSIONS AND RECOMMENDATIONS

Productivity of white-tailed deer in New Hampshire has not declined since the 1980s despite a substantial increase in density, and declining recruitment indices from harvested deer suggest that summer fawn mortality has increased. Similar patterns were observed in other nearby jurisdictions, providing additional evidence that decline in recruitment indices is related to exogenous factors such as predation, winter severity, or gradual change in hunter selectivity. The following should aid managers in assessing the factors limiting population growth in the northeast.

I. Productivity of White-tailed Deer in New Hampshire

1) Fawn pregnancy rate was 8%, which is typical of most northern deer populations, while 100% of yearlings and 97% of adults were pregnant. Fecundity of yearlings (1.72 fetuses/pregnant doe) and adults (1.95) were relatively high for areas without extensive agriculture and indicate a healthy and productive population.
2) Median breeding date was 20 November for adults, 26 November for yearlings, and 18 December for fawns. The breeding period spanned from 3 November–8 January, but 77% of deer bred from 10 November–5 December. This breeding period was similar to other northern populations and nearly identical to that observed during the early 1950s in New Hampshire. The concise breeding period and high pregnancy rates indicate that breeding ecology has not been impacted by male-biased harvest.
3) Productivity of adults and yearlings has not changed since the 1980s, but fawn pregnancy rate declined 68%. Conservative antlerless harvest since 1983 led to a

higher proportion of adults in the population during 2011-2013; this resulted in an 18% increase in potential recruitment.

4) Stable or increased productivity and declining recruitment indices suggest that summer fawn mortality has increased. Possible causes include increased population density in specific regions, winter severity that periodically reduces productivity, and direct predation of fawns by higher predator populations. Field studies will be necessary to accurately determine the rate and cause of summer fawn mortality.

5) Gradual change in hunter selectivity could bias recruitment indices from harvested deer. A survey of hunter attitudes regarding the harvest of fawns and other antlerless deer would provide a better understanding of hunter selectivity and improve the utility of these indices.

II. Influence of Winter Weather on Nutritional Condition of White-tailed Deer in New Hampshire

6) Fecal glucocorticoid concentration (fGC) did not exhibit any trend over winter and was not a useful predictor of marrow fat content. It is possible that opportunistic collection of samples from incidentally killed animals caused biased estimates. Collection of feces from the field would avoid this problem and allow for larger sample size; temporal patterns and relationships with weather conditions will provide equally valuable insight into relationships between nutritional condition and fGC.

7) Marrow fat (MF) declined through winter; all fawns and 62% of adults collected after 1 April had MF <80%, indicating depletion of energy reserves and poor

nutritional condition. This did not vary among years despite substantial differences in WSI. There were no significant differences in the rate of fat loss among age classes, but fawns began losing MF earlier than older deer.

8) The WSI, particularly duration of deep snow, affects the rate of MF loss. More deer had MF <10% (presumably indicating starvation was imminent) in 2011 (WSI = 60) than 2012 (13) or 2013 (16). Because WSI is related to annual variation in nutritional condition, continued monitoring is warranted.

9) It is critical that managers also consider the timing of severe winter conditions when interpreting the WSI. If deep snow persists in April when most deer have depleted their energy reserves and the energy cost of gestation increases exponentially, mortality, malnutrition, and reduced productivity will be more severe than predicted by WSI alone.

III. Productivity, Recruitment, and Physical Characteristics of White-tailed Deer in Northeastern North America

10) Despite varying trends in deer density since the 1980s, yearling male weight increased consistently in Vermont, Maine, and New Brunswick, and remained stable in New Hampshire; there were no differences among time periods in YABD, yearling female weight, or fawn weight in any jurisdiction. Substantial changes in density were not concurrent with change in physical condition of deer in these populations; however, density was always low (<6 deer/km^2) and presumably well below summer carrying capacity.

11) There was no change in productivity of adults among time periods in any jurisdiction, but fawn pregnancy rates declined throughout the region and yearling productivity declined in Maine and New Brunswick.

12) Recruitment based on fawn:doe ratio in the harvest declined consistently in Vermont, New Hampshire, and New Brunswick, and during the most recent time periods in Maine. Population productivity has probably remained stable or increased throughout the region (see number 3), suggesting that summer fawn mortality has increased.

13) Field studies will be necessary to accurately determine the rate and cause of summer fawn mortality. Gradual change in hunter selectivity could also bias recruitment indices from harvested deer and may explain a portion of the decline in fawn:doe ratio. A survey of hunter attitudes regarding the harvest of fawns and other antlerless deer would provide a better understanding of hunter selectivity and improve the utility of these indices.

14) These populations may be near or above the carrying capacity of winter range in many years. The relative condition and availability of DWAs has declined throughout much of the region since the 1980s, which has presumably reduced winter carrying capacity. Increased competition for limited winter forage could cause reduced nutritional condition in spring and result in higher neonatal mortality and reduced productivity of younger age classes. Accurate and updated mapping of DWAs, knowledge of the quantity and extent of supplemental feeding, and estimates of winter K will provide valuable insight into the factors limiting these populations.

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APPENDICES

APPENDIX A. DATA FROM SAMPLED DEER

Table A.1. Kill date, region, age class, % marrow fat (MF), fecal glucocorticoid concentration (FGC), corpora lutea (CL), pregnancy status, number of fetuses, and estimated fetal age of 249 female deer collected December–May, 2010-2013.

ID	Kill Date	Region	Age Class	MF (%)	FGC (ng/g)	CL	Pregnant	Fetuses[1]	Fetal Age (days)
11001	12/14/2010	S	Y			1	Yes	1	40
11002	1/15/2011	S	F	84.5		1	Yes	1	30
11003	1/7/2011	N	A	89.1		0	No	0	
11004	1/4/2011	SC	A	87.5		1	Yes		
11005	2/9/2011	SC	A			2	Yes	2	96
11006	1/19/2011	S	A	92.5		2	Yes	1	48
11007	1/18/2011	S	A	82.8		2	Yes	2	62
11008	2/10/2011	SC	A	87.8		0	No	0	
11009	2/5/2011	S	A	89.4		3	Yes	3	80
11010	1/10/2011	SC	F	83.9		0	No	0	
11011	1/6/2011	S	F	95.4			Unk		
11012	1/4/2011	S	A	89.4			Unk		
11013	2/23/2011	S	A	61.5		2	Yes	1	45
11014	2/28/2011	SC	F	68.9		0	No	0	
11015	2/4/2011	S	Y	87.5			Yes	2	74
11016	2/15/2011	S	A	86.6		2	Yes	2	78
11017	3/2/2011	S	A			2	Yes	2	104
11018	3/1/2011	S	A	89.7		2	Yes	1	85
11019	2/18/2011	S	Y	63.9		2	Yes	2	103
11020	2/28/2011	N	A	88.8		2	Yes	2	94
11021	3/3/2011	S	F	28.8		0	No	0	
11022	3/4/2011	SC	A	86.4		2	Yes	2	105
11023	3/8/2011	S	A	81.7		2	Yes		
11024	3/9/2011	SC	A	84.1		2	Yes	2	113
11025	3/11/2011	SC	A	81.3		2	Yes	2	123
11026	3/11/2011	S	A	71.1		2	Yes	2	114
11027		N	F				No	0	
11028	3/16/2011	S	A	72.5		3	Yes	3	119
11029	3/16/2011	S	A	84.9			Unk		
11030	3/16/2011	S	A	48.8		2	Yes	2 (1)	117
11031	3/6/2011	N	A	88.6		2	Yes	2	114
11032	3/6/2011	N	A	74.5		2	Yes	2	104
11033	3/15/2011	SC	F	39.1		0	No	0	
11034	3/16/2011	N	A	83.6		2	Yes	2	115
11035	3/9/2011	S	A	61.9		3	Yes	3	110
11036	2/14/2011	N	F	80.8		0	No	0	

Table A.1. Kill date, region, age class, % marrow fat (MF), fecal glucocorticoid concentration (FGC), corpora lutea (CL), pregnancy status, number of fetuses, and estimated fetal age of 249 female deer collected December–May, 2010-2013.

ID	Kill Date	Region	Age Class	MF (%)	FGC (ng/g)	CL	Pregnant	Fetuses[1]	Fetal Age (days)
11037	3/11/2011	N	F	42.9		0	No	0	
11038	3/9/2011	S	A	78.4		3	Yes	3	115
11039	3/10/2011	S	A			3	Yes	1	103
11040	3/7/2011	S	A	81.9		2	Yes	1	102
11041	3/16/2011	SC	A	84.5		2	Yes	2	118
11042		N	A	81.8		3	Yes	2	97
11043	3/16/2011	S	A			2	Yes	2	122
11044	3/17/2011	S	A	86.5		2	Yes		111
11045	3/20/2011	S	F				No	0	
11046	3/12/2011	S	A	80.7		2	Yes	2	112
11047	3/13/2011	.	A			2	Yes	2	116
11048	3/16/2011	S	A			2	Yes	2	107
11049	3/25/2011	N	F	11.9		0	No	0	
11050	3/24/2011	N	A	11			Unk		
11051	3/24/2011	S	A			2	Yes	2	121
11052	3/24/2011	S	A			1	Yes	1	119
11053	3/26/2011	S	1+			2	Yes	1	117
11054	3/28/2011	S	A				Yes	1	114
11055	3/26/2011	S	F			0	No	0	
11056	3/28/2011	S	A			2	Yes	2	142
11057	3/26/2011	N	A	62		2	Yes	2	124
11058	3/22/2011	S	A	87.2		2	Yes	2	111
11059	3/25/2011	S	A	85.8		3	Yes	3	130
11060	3/28/2011	S	F			0	No	0	
11061	3/22/2011	S	F				Unk		
11062	2/28/2011	S	Y	82.9			Yes	2	87
11063	3/21/2011	S	A	79.9		2	Yes	2	124
11064	3/10/2011	S	Y				Yes	2	102
11065	2/4/2011	S	F	84.3		0	No	0	
11066	2/15/2011	S	A	82.5		1	Yes	1 (0)	
11067	3/14/2011	S	A	94.7			Yes	2	103
11068			1+				Yes	2	114
11069			1+				Yes	2	123
11070	3/31/2011	SC	F	51.4		0	No	0	
11071	3/25/2011	S	A	85.8		3	Yes	2 (0)	
11072	4/3/2011	SC	A	89.4		2	Yes	2	140
11073	3/27/2011	N	A	39.5		3	Yes	3 (0)	
11074	3/28/2011	N	Y	58.5		2	Yes	2	126

Table A.1. Kill date, region, age class, % marrow fat (MF), fecal glucocorticoid concentration (FGC), corpora lutea (CL), pregnancy status, number of fetuses, and estimated fetal age of 249 female deer collected December–May, 2010-2013.

ID	Kill Date	Region	Age Class	MF (%)	FGC (ng/g)	CL	Pregnant	Fetuses[1]	Fetal Age (days)
11075	3/31/2011	N	A	55.8			Yes	1	134
11076	3/28/2011	S	F	80		0	No	0	
11077	3/28/2011	S	A	82.3		2	Yes	2	133
11078	3/29/2011	N	A	54.8		2	Yes	2	132
11079	3/29/2011	S	F			0	No	0	
11080	3/28/2011	S	F			0	No	0	
11081	4/4/2011	S	A			3	Yes	3	136
11082	4/4/2011	S	A			3	Yes	3	139
11083	3/16/2011	S	A				Yes	2	109
11084	4/18/2011	S	F	64.9		0	No	0	
11085	4/11/2011	S	F	15.4		0	No	0	
11086	4/12/2011	N	Y				Yes	1	136
11087	4/8/2011	S	A	85.6		2	Yes	2	139
11088		SC	1+			2	Yes	2	150
11089		SC	A	88.8			Yes	1	136
11090	4/7/2011	S	A	93.3		3	Yes	3	137
11091	4/17/2011	SC	A	67.8		2	Yes	2	148
11092	4/12/2011	N	A	1.4		2	Yes	2	136
11093	4/9/2011	S	A	67.8			Yes	2	140
11094	3/14/2011	S	Y	91.3		1	Yes	1	109
11095	4/9/2011	S	Y	48.4			Yes	2	133
11096	4/12/2011	S	A	88.2		2	Yes	2	138
11097	4/7/2011	N	1+			2	Yes	1	147
11098	4/5/2011	N	Y	80.3		2	Yes	2	136
11099	4/7/2011	S	A	63.4		2	Yes	2	140
11100	4/6/2011	N	A	22.1		2	Yes	2	136
11101	4/6/2011	N	A	68.2			Yes	2	141
11102	4/7/2011	N	A	2		3	Yes		130
11103	4/5/2011	N	A	50.4		1	Yes	0	
11104	4/1/2011	N	F	9.5		0	No	0	
11105	4/5/2011	N	F	2.2		0	No	0	
11106	4/6/2011	N	A	2.1		2	Yes	2	117
11107	4/8/2011	N	Y	17.5		2	Yes	2	110
11108	3/21/2011	N	A	82.3			Yes	3	99
11109	4/25/2011	S	A				Yes	2	155
11110	4/2/2011	S	A	84.7		2	Yes	2	99
11111	4/28/2011	S	F			0	No	0	
11112	4/17/2011	N	Y	55.3			Yes	2	118

Table A.1. Kill date, region, age class, % marrow fat (MF), fecal glucocorticoid concentration (FGC), corpora lutea (CL), pregnancy status, number of fetuses, and estimated fetal age of 249 female deer collected December–May, 2010-2013.

ID	Kill Date	Region	Age Class	MF (%)	FGC (ng/g)	CL	Pregnant	Fetuses[1]	Fetal Age (days)
11113	4/16/2011	N	A	68.9		2	Yes	1	152
11114	4/25/2011	S	A	71.2			Yes		
11115	1/4/2011	S	F	81.1		0	No	0	
11116	5/6/2011	SC	A	90.7		3	Yes	2	157
11117	5/19/2011	S	A	61.5		3	Yes	3	173
11118	4/25/2011	S	A	84.9		2	Yes	2	168
11119	4/12/2011	S	A	85.5		2	Yes	2	112
11120	4/21/2011	N	A			2	Yes	2	166
11121	5/16/2011	S	F	47.4		0	No	0	
11122	5/4/2011	N	F	2.2		0	No	0	
11123	4/5/2011	N	F	10.7		0	No	0	
11124	4/29/2011	N	A			2	Yes	2	160
11125	4/26/2011	N	A	8.2			Yes		
11126	4/15/2011	N	A				Yes	1	139
11127	4/27/2011	N	A				Yes	3	140
12001	1/4/2012	SC	F	83.7	571	1	Yes		
12002	1/9/2012	N	A		2681	0	No	0	
12003	1/11/2012	N	A		1261	2	Yes		
12004	1/30/2012	S	F	91.5	149	0	No	0	
12005	1/20/2012	S	Y	79.8	1907	1	Unk		
12006	1/28/2012	N	A	87		2	Unk		
12007	2/22/2012	SC	A	85.4	669	2	Yes	2	78
12008	2/1/2012	S	F		197	0	No	0	
12009	1/25/2012	S	F	76.1	1417	0	No	0	
12010	1/20/2012	S	F	77.7		0	No	0	
12011	2/8/2012	N				2	Yes	2	87
12012	2/14/2012	N	A		687	3	Yes	3	94
12013	2/10/2012	N	A	91.3	288	2	Yes		79
12014	2/21/2012	N	F	73.2	776	0	No	0	
12015	2/6/2012	N	F	82.8	183		Unk		
12016	3/4/2012	SC	A	88.5			Yes	2	99
12017	3/9/2012	S	A	88.8	1247	2	Yes	2 (0)	
12018	2/27/2012	SC	A				Yes	2	95
12019	3/12/2012	SC	F	89.2		0	No	0	
12020	3/9/2012	N	F	73.5	2154	0	No	0	
12021	2/29/2012	S	A	90.1		2	Yes	2	92
12022	3/9/2012	S	A	83		2	Yes	2	116
12023	2/23/2012	S	Y	83.6	972	1	Yes	1	99

Table A.1. Kill date, region, age class, % marrow fat (MF), fecal glucocorticoid concentration (FGC), corpora lutea (CL), pregnancy status, number of fetuses, and estimated fetal age of 249 female deer collected December–May, 2010-2013.

ID	Kill Date	Region	Age Class	MF (%)	FGC (ng/g)	CL	Pregnant	Fetuses[1]	Fetal Age (days)
12024	3/20/2012	N	F		1204		No	0	
12025	4/4/2012	N	A	91.8		2	Yes	2	144
12026	3/14/2012	N	A	89.3		2	Yes	2	115
12027	3/11/2012	N	Y	76.7		3	Yes	3	100
12028	4/4/2012	SC	A	73.9	539	2	Yes	2	148
12029	3/29/2012	N	A	56.1		3	Yes	1	131
12030	3/20/2012	S	A		1132	1	Yes	1	118
12031	4/4/2012	SC	Y	80.3	494	1	Yes	1	110
12032	2/29/2012	N	A	83.5	2316		Yes		
12033	2/26/2012	N	A	85.9	163	2	No	0	
12034	3/14/2012	N	A	90.7			Yes	3	119
12035	4/15/2012	S	A	79.1	344	2	Yes	2	122
12036	4/2/2012	S	F	58.1		0	No	0	
12037	3/21/2012	S	A	59.8	1023	3	Yes	2	113
12038	4/30/2012	S	F	31.4	957	0	No	0	
12039	4/16/2012	N	F	36.8	958	0	No	0	
12040		S	A				Yes	1	87
12041			F	63.1	284	0	No	0	
12042	5/7/2012	S	A				Yes	2	149
12043	1/13/2012	S	A			2	Yes	1	42
12044	12/29/2011	S	Y			2	Yes	2	46
12045	4/20/2012	S	A				Yes	1	134
12046	3/17/2012	N	A	92.7			Yes	2	112
12047	5/3/2012	S	F	26.6	1626	0	No	0	
12048	2/19/2012	S	F	78	2778	0	No	0	
12049	1/17/2012	S	F	72.8	2658	0	No	0	
12050	3/15/2012	N	A	79.16		1	Yes	1	91
12051	2/22/2012	SC	A	88.26		2	Yes	2	75
13001	1/10/2013	S	F	91.4		0	No	0	
13002	1/10/2013	SC	F	85.9		0	No	0	
13003	1/9/2013	SC	F	83.35		0	No	0	
13004	1/11/2013	SC	F				Yes		
13005	1/4/2013	SC	F	89.19		0	No	0	
13006	1/21/2013	SC	F	86.04		0	No	0	
13007	1/10/2013	SC	F	83.1		1	Yes	1	
13008	1/4/2013	SC	F			0	No	0	
13009	1/24/2013	S	F	81.54			Unk		
13010	1/13/2013	SC	A	89.44	259	1	Yes	1	37

Table A.1. Kill date, region, age class, % marrow fat (MF), fecal glucocorticoid concentration (FGC), corpora lutea (CL), pregnancy status, number of fetuses, and estimated fetal age of 249 female deer collected December–May, 2010-2013.

ID	Kill Date	Region	Age Class	MF (%)	FGC (ng/g)	CL	Pregnant	Fetuses[1]	Fetal Age (days)
13011	1/24/2013	S	A	88		2	Yes	2	63
13012	1/31/2013	S	A	89.92			Unk		
13013	1/24/2013	S	1+			2	Yes		
13014	1/22/2013	S	A			2	Yes	2	65
13015	1/7/2013	S	A		426	2	Yes		43
13016	1/15/2013	S	A		2434	2	Yes	2	42
13017	1/30/2013	N	A	90.9	230	3	Yes		66
13018	2/6/2013	S	A	80.7			Yes		84
13019	1/23/2013	N	A	2.7			Unk		
13020	2/13/2013	N	Y		810	2	Yes		53
13021	1/20/2013	N	F	65.4	436		No	0	
13022	12/19/2012	N	A	87.38	2796	2	Yes	2	42
13023	2/13/2013	SC	F	70.4	276		Unk		
13024	3/8/2013	S	F	70.6	315	0	No	0	
13025	2/6/2013	N	A		961	2	Yes	1	69
13026	2/13/2013	N	A		682	3	Yes	3	60
13027	3/7/2013	N	F	76.42	204	2	Yes	1	77
13028	3/8/2013	S	F	60.85	221	0	No	0	
13029	3/18/2013	S	F	53.47	299	0	No	0	
13030	4/1/2013	SC	A	91.81			Yes	2	140
13031	3/28/2013	SC	F	87.11		0	No	0	
13032	3/6/2013	N	F	71.21	807	0	No	0	
13033	3/11/2013	S	A				Yes	2	119
13034	3/13/2013	S	A			2	Yes	2	114
13035	3/11/2013	S	A				Yes	2	114
13036	2/15/2013	N	A			1	Yes	2	90
13037	3/14/2013	N	A	78.34	397	2	Yes	2 (1)	98
13038	4/1/2013	S	A	70.93			Yes	2	135
13039	3/6/2013	N	A		156	1	Yes	1	100
13040	4/1/2013	S	A	40.35		2	Yes	2	107
13041	3/5/2013	N	A	87.58	263	3	Yes	3	98
13042	3/4/2013	N	1+		263		Yes	2	119
13043	3/16/2013	N	A	81.08	759	2	Yes	1	115
13044	4/23/2013	S	F	53.16	399	0	No	0	
13045	4/24/2013	N	A	86.27		2	Yes	2	131
13046	3/26/2013	N	A			2	Unk		
13047	2/16/2013	S	F	78.02	1614	0	No	0	
13048	4/8/2013	N	A	59.97			Yes	2	146

Table A.1. Kill date, region, age class, % marrow fat (MF), fecal glucocorticoid concentration (FGC), corpora lutea (CL), pregnancy status, number of fetuses, and estimated fetal age of 249 female deer collected December–May, 2010-2013.

ID	Kill Date	Region	Age Class	MF (%)	FGC (ng/g)	CL	Pregnant	Fetuses[1]	Fetal Age (days)
13049	4/9/2013	S	A	77.1			Yes	1	133
13050	4/5/2013	S	A	3.2	1119		Yes	2 (0)	
13051	2/26/2013	N	A	88.67	145		Yes	2	103
13052	4/5/2013	S	A	74.37			Yes	2	127
13053	4/13/2013	S	A	82.44			Yes	2	136
13054	3/24/2013	N	A				Yes	2	128
13055	3/23/2013	N	A			2	Yes	2	122
13056	3/27/2013	S	A				Yes	2	134
13057	4/12/2013	S	A			2	Yes	2	124
13058	3/27/2013	S	A		594	3	Yes	3	126
13059	4/25/2013	S	A			2	Yes	2	165
13060	3/26/2013	S	1+			2	Yes		
13061	3/20/2013	N	F			0	No	0	
13062	3/30/2013	N	A	85.85	3297	2	Yes	2	124
13063	4/19/2013	N	A	80.03	995	2	Yes	1	142
13064	4/10/2013	N	A	50.13	956	2	Yes	1	137
13065	4/9/2013	N	A	80.11	1968	2	Yes	2	140
13066	3/27/2013	N	A	37.88	1097	2	Yes	2	118
13067	3/27/2013	N	Y		204	1	Yes	1	104
13068	4/4/2013	N	A	73.83	673	3	Yes	3	136
13069	4/9/2013	SC	Y	60.71			Yes	2	145
13070	4/4/2013	SC	A				Yes	1	148
13071	4/9/2013	N	A	89.83	567	3	Yes	3	139

[1] Numbers in parentheses indicate the number of viable fetuses if ≥1 fetus was being resorbed.

APPENDIX B. WEATHER STATIONS USED TO CALCULATE THE WINTER SEVERITY INDEX

Table B.1. Weather stations used to calculate the winter severity index for each wildlife management unit (WMU) by the New Hampshire Fish and Game Department (NHFG) and in this study. Station numbers correspond to the map in Figure B.1.

			Used for WMUs	
#	Station Name	WMU	by NHFG	in this study
1	ALEXANDRIA 4	G2		G2
2	BATH 3	D2		D2W
3	BENTON 5 SW	D2	D2E, D2W, F, G1, G2	D2E, D2W
4	BERLIN MUNICIPAL AIRPORT	C2		C2
5	BERLIN	C2	C2	C1, C2
6	BETHLEHEM 2	D1		D1, E
7	BRADFORD 2	I2		I2
8	CONCORD MUNICIPAL AIRPORT	L	I1, I2, J2, K, L	I1, J2, K, L
9	DURHAM 2 N	L		L
10	DURHAM 2 SSW	L		L
11	DURHAM	L	L	L
12	EAST MILFORD	K		K, M
13	EPPING	L		L, M
14	ERROL	A	B, C2	A, B, C2
15	FIRST CONNECTICUT LAKE	A	A, C1, E	A
16	FITZWILLIAM 2 W	H2		H2
17	FRANCESTOWN	K		K, M
18	FRANKLIN FALLS DAM	I1		I1, J2
19	GLENCLIFF 2	D2E		D2E, D2W, F
20	GORHAM 3	E		C1, C2, E
21	GREENLAND	M	M	M
22	GREENVILLE 1 NNE	K	K, M	K, M
23	HANOVER	G1	D2W, G1, G2, H1, I1, I2	G1
24	HOPKINTON LAKE	I2		I1, I2, K
25	HUDSON 1 SSE	M		M
26	JAFFREY MUNICIPAL AIRPORT	K		H2, K
27	JAFFREY SILVER RANCH AIRPARK	K		H2, K
28	JEFFERSON	D1		C1, D1, E
29	KEENE	H2	H2, K	H2
30	LAKEPORT 2	J2		J2
31	LANCASTER	D1	B, C1, D1, D2W	D1, C1
32	LEBANON MUNICIPAL AIRPORT	H1		G1, H1
33	MACDOWELL DAM	H2		H2, K
34	MANCHESTER AIRPORT	M		L, M
35	MASSABESIC LAKE	M		L, M

Table B.1. Weather stations used to calculate the winter severity index for each wildlife management unit (WMU) by the New Hampshire Fish and Game Department (NHFG) and in this study. Station numbers correspond to the map in Figure B.1.

			Used for WMUs	
#	Station Name	WMU	by NHFG	in this study
36	MEREDITH 3 NNE	J2		J1, J2
37	MOUNT SUNAPEE	I2		I2
38	NASHUA 2 NNW	M		M
39	NEW DURHAM 3 NNW	J2		J1, J2
40	NEW HAMPTON 2	I1		G2, I1, J2
41	NEWPORT	H1		H1, I2
42	NORTH CONWAY	E	C1, E, J1	E, J1
43	NORTH HAMPTON	M		M
44	OTTER BROOK LAKE	H2		H2
45	PINKHAM NOTCH	E		E
46	ROCHESTER	L		J2, L
47	ROCHESTER SKYHAVEN AIRPORT	L		J2, L
48	SURRY MOUNTAIN LAKE	H2		H2
49	TAMWORTH 4	J1	D2E, F, G2, J1	F, J1
50	WALPOLE 3	H2		H1, H2
51	WENTWORTH	D2		D2W, F, G1
52	WEST HEMPSTEAD	M	L, M	M
53	WHITEFIELD	D1		D1
54	YORK POND	C1		C1
55	COLEBROOK	B	B, C2	A,B

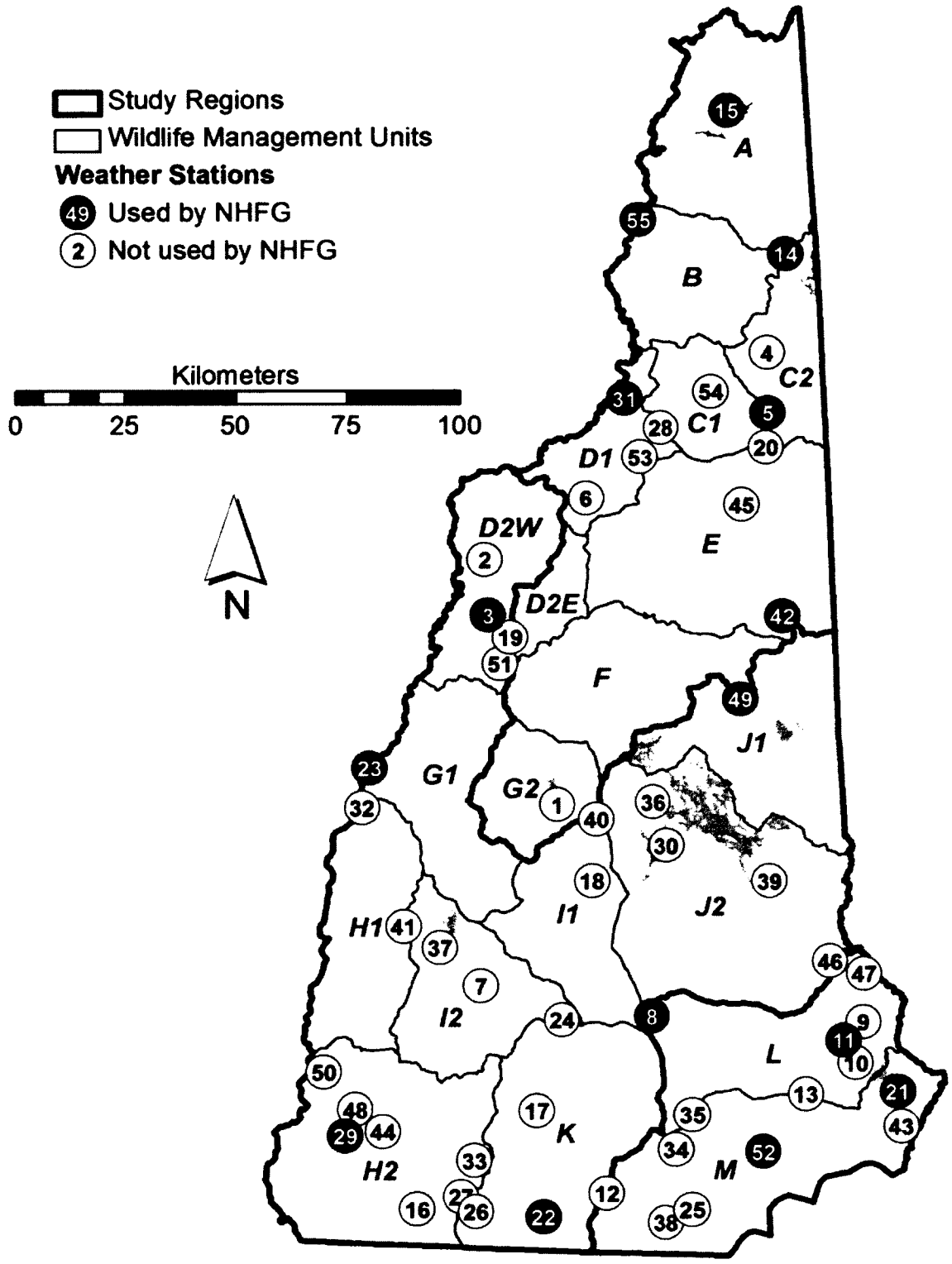

Figure B.1. Location of 55 NOAA weather stations used in this study to calculate a winter severity index (WSI) for each wildlife management unit. Stations with black circles are used by the New Hampshire Fish and Game Department to calculate WSI. Station numbers correspond to Table B.1.

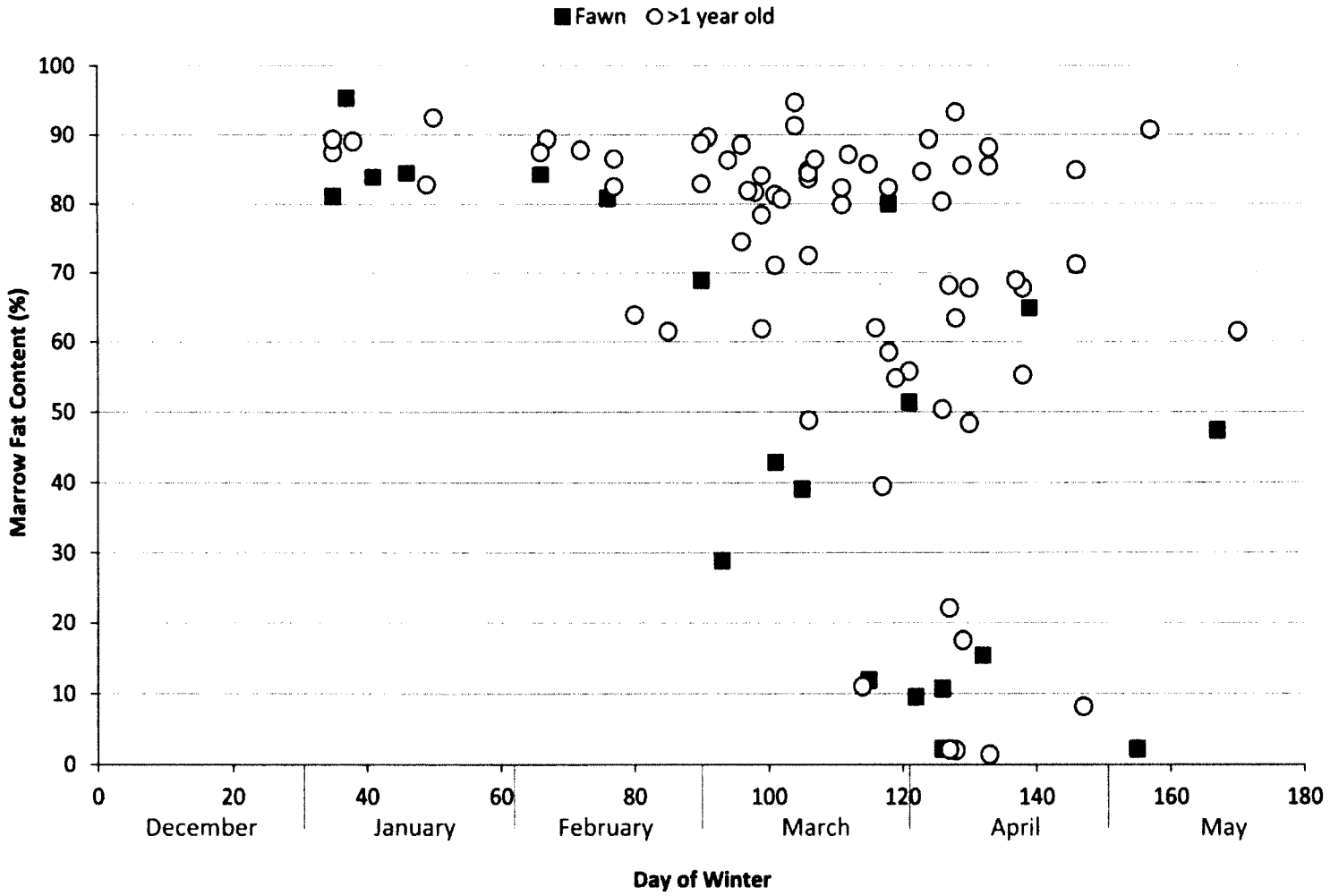

Figure C.1. Temporal pattern of marrow fat content of 91 female white-tailed deer collected during December–May, 2010-2011. Marrow fat content >80% indicates no loss of marrow fat; <10% presumably indicates starvation was imminent.

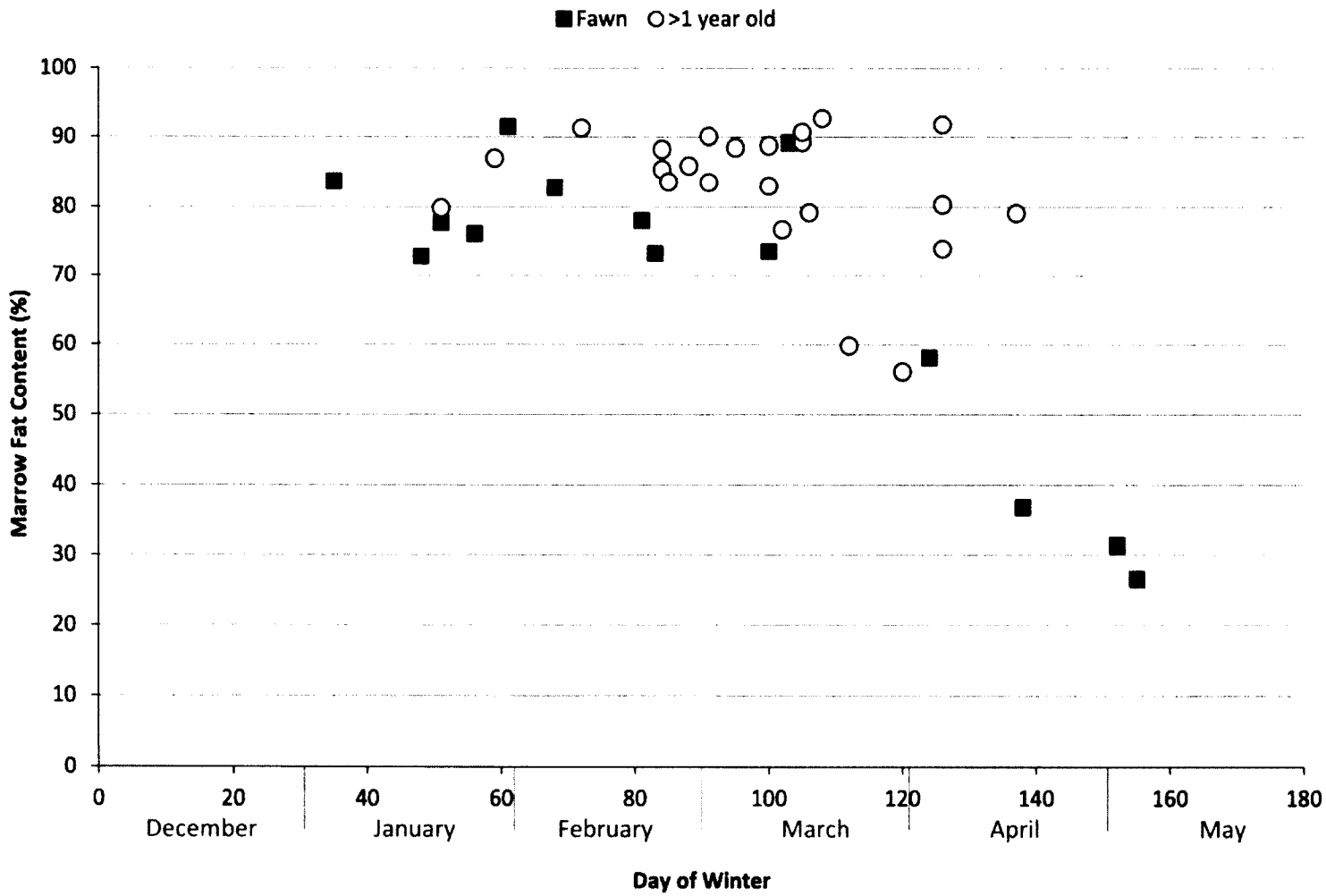

Figure C.2. Temporal pattern of marrow fat content of 38 female white-tailed deer collected during December–May, 2011-2012. Marrow fat content >80% indicates no loss of marrow fat; <10% presumably indicates starvation was imminent.

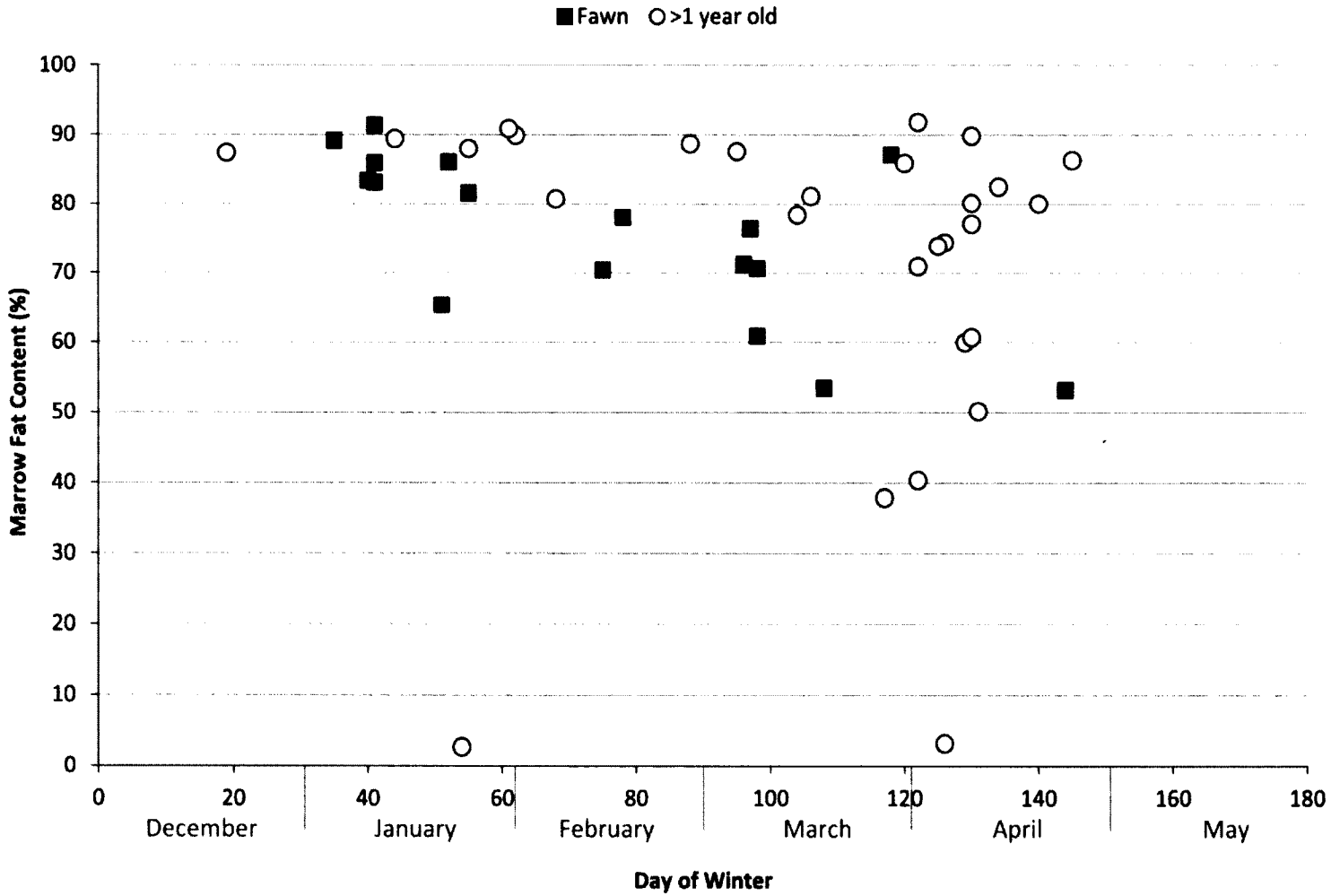

Figure C.3. Temporal pattern of marrow fat content of 45 female white-tailed deer collected during December–May, 2012-2013. Marrow fat content >80% indicates no loss of marrow fat; <10% presumably indicates starvation was imminent.

APPENDIX D. REGIONAL PRODUCTIVITY DATA

Table D.1. Pregnancy and fecundity data from Maine, New Brunswick, New Hampshire, and Vermont used for regional analyses.

	Pregnancy				Fecundity (fetuses/pregnant doe)			
Year	**Fawn**	**Yearling**	**Adult**	**≥1**	**Fawn**	**Yearling**	**Adult**	**≥1**
Maine								
2011	0.10	0.57	0.98	0.93	1.00	1.25	1.92	1.88
2012	0.00			0.87				1.85
New Brunswick								
2001	0.14	0.87	0.94	0.92	1.50	1.69	1.84	1.81
2002	0.08	0.70	0.78	0.77	1.25	1.41	1.77	1.70
2003	0.10	0.81	0.88	0.86	1.20	1.36	1.86	1.74
2004	0.02	0.66	0.85	0.78	1.00	1.31	1.68	1.57
2005	0.09	0.71	0.88	0.84	1.00	1.35	1.84	1.73
2006	0.09	0.77	0.79	0.79	1.00	1.38	1.70	1.60
2007	0.04	0.74	0.82	0.80	1.00	1.51	1.88	1.80
2008	0.06	0.71	0.77	0.76	1.27	1.38	1.72	1.64
2009	0.02	0.70	0.88	0.85	1.00	1.26	1.82	1.74
2010	0.00	0.61	0.82	0.77		1.20	1.79	1.69
New Hampshire								
1972	0.14	0.60	0.97	0.92	1.00	1.67	1.68	
1975	0.05	0.79	0.81	0.80	1.00	1.45	1.85	1.73
1976	0.00	0.83	0.86	0.85		1.60	1.92	1.82
1977	0.19	0.64	1.00	0.87	1.00	1.57	1.84	1.77
1978	0.00	0.67	0.83	0.80		1.83	1.91	1.90
1979	0.00	0.90	0.89	0.89		1.33	1.54	1.48
1980	0.13	0.67	0.86	0.82	1.00	2.00	1.83	1.86
1981	0.37	1.00	1.00	1.00	1.00	2.00	2.00	2.00
1982	0.35	1.00	0.85	0.89	1.00	1.64	1.65	1.65
1983	0.19	0.86	0.89	0.88	1.25	1.58	1.79	1.69
1984	0.22	1.00	0.86	0.89	1.25	1.80	1.92	1.88
1985	0.09	0.94	0.93	0.93	1.00	1.88	1.73	1.79
1986	0.26	1.00	0.92	0.95	1.00	1.33	1.67	1.52
1987		1.00	0.96	0.96	1.00	1.50	1.84	1.81
2011	0.04	1.00	0.97	0.98	1.00	1.75	1.99	1.93
2012	0.06	1.00	0.92	0.94		1.75	1.85	1.83
Vermont								
1999	0.07			0.93	1.00			1.95
2001	0.05			0.95	1.67			1.75
2004	0.03			0.92	1.00			1.52
2008	0.00			0.92				1.60
2009	0.00			0.94				1.86
2011	0.00			0.78				1.61
2012	0.00			0.81				1.48

APPENDIX E. REGIONAL HARVEST DATA

Table E.1. Biological data from harvested deer, harvest fawn:doe ratio, and adult male harvest density from Maine, 1970–2012.

	Yearling				Fawn			Adult
	Antler		Weight (kg)		Weight (kg)		Fawn:Doe	Male
Year	BD (mm)	Points	Male	Female	Male	Female	Ratio	Harvest/km^2
1970	16.9						0.55	0.19
1971	15.4						0.52	0.12
1972	15.8						0.53	0.17
1973	16.8						0.52	0.15
1974	17.7						0.51	0.20
1975	16.2						0.48	0.21
1976	16.4						0.44	0.18
1977	16.8						0.50	0.18
1978	16.6						0.46	0.17
1979	16.5						0.50	0.16
1980	17.8						0.46	0.22
1981	18.2						0.48	0.19
1982	17.4						0.50	0.17
1983	17.1						0.52	0.16
1984	17.4						0.43	0.16
1985	17.8						0.43	0.19
1986	18.0						0.33	0.19
1987	17.7						0.54	0.19
1988	17.4						0.51	0.21
1989	17.4						0.51	0.21
1990	17.4						0.46	0.19
1991	17.6						0.48	0.21
1992	17.6						0.51	0.21
1993	17.7						0.47	0.21
1994	17.5						0.47	0.20
1995	17.9						0.47	0.22
1996	17.1						0.43	0.25
1997	17.4						0.57	0.25
1998	18.4						0.55	0.22
1999	18.0	3.4	51.7	44.5	29.9	27.2	0.58	0.24
2000	17.8	3.4	51.3	44.5	29.9	28.6	0.54	0.27
2001	17.7	3.3	51.7	44.5	30.4	27.2	0.50	0.21
2002	18.1	3.5	50.8	43.5	31.3	28.1	0.54	0.26
2003	17.5	3.2	51.3	44.0	29.9	27.2	0.60	0.20
2004	17.3	3.1	49.9	41.7	29.0	26.8	0.49	0.22
2005	17.3	3.2	53.6	44.0	30.9	28.4	0.53	0.19

Table E.1. Biological data from harvested deer, harvest fawn:doe ratio, and adult male harvest density from Maine, 1970–2012.

	Yearling				Fawn			Adult
	Antler		Weight (kg)		Weight (kg)		Fawn:Doe	Male
Year	BD (mm)	Points	Male	Female	Male	Female	Ratio	Harvest/km^2
2006	18.2	3.5	55.0	44.7	30.5	27.4	0.56	0.20
2007	17.4	3.1	52.9	42.8	28.7	26.2	0.50	0.20
2008	17.5	3.3	52.0	45.3	29.6	27.2	0.45	0.17
2009	17.6	3.2	52.4	44.3	31.6	28.1	0.51	0.14
2010	18.5	3.6	55.4	45.1	32.0	28.3	0.50	0.15
2011	18.0	3.6	55.0	45.7	29.9	27.9	0.48	0.15
2012	18.2	3.4	54.4	43.9	30.3	27.2	0.42	0.19

Table E.2. Biological data from harvested deer, harvest fawn:doe ratio, and adult male harvest density from New Brunswick, 1980–2012.

	Yearling				Fawn			Adult
	Antler		Weight (kg)		Weight (kg)		Fawn:Doe	Male
Year	BD (mm)	Points	Male	Female	Male	Female	Ratio	Harvest/km^2
1980	18.7		53.1	44.5			0.59	0.13
1981	17.9		54.0	45.8			0.60	0.15
1982	17.5		52.2	44.5			0.63	0.15
1983	17.8		51.3	44.0			0.59	0.18
1984	16.9		51.3	44.9			0.61	0.17
1985	17.3		51.3	44.9			0.55	0.21
1986	17.2		53.5	47.2			0.52	0.20
1987	18.9		55.3	46.3			0.60	0.17
1988	18.0		53.1	46.3			0.53	0.15
1989	17.0		52.2	43.5			0.55	0.14
1990	16.7		55.0	48.0			0.36	0.10
1991	18.1		54.0	48.0			0.39	0.10
1992	18.5		54.0	47.0			0.40	0.09
1993	17.8		53.0	45.0			0.37	0.09
1994	17.9		54.0	46.0			0.34	0.08
1995	19.4		55.0	46.0			0.37	0.09
1996	16.8		50.0	44.0			0.41	0.11
1997	17.9		54.0	47.0			0.37	0.10
1998	18.6		53.2	46.5			0.36	0.09
1999	18.9		56.3	47.5			0.35	0.07
2000	19.0		55.5	45.9	31.3	26.8	0.34	0.07
2001	19.0		56.9	48.8	29.5	27.7	0.28	0.05
2002	19.0		53.0	40.4	27.7	20.9	0.30	0.08
2003	19.4		56.0	46.8	33.6	29.9	0.25	0.07
2004	18.3		56.4	49.3	29.9	30.8	0.23	0.08
2005	18.8		57.3	47.6	32.2	32.7	0.22	0.08
2006	18.0		58.0	48.0	29.5	28.1	0.20	0.11
2007	17.9		57.6	49.0	31.3	27.7	0.20	0.11
2008	17.6		58.0	50.0	30.8	29.5	0.19	0.09
2009	17.6		57.0	49.0	31.3	28.1	0.23	0.05
2010	19.0		58.0	45.0	33.6	32.7	0.28	0.05
2011	18.2		59.0	50.0	29.9	29.9	0.24	0.06
2012	18.5		58.7	49.2				0.07

Table E.3. Biological data from harvested deer, harvest fawn:doe ratio, and adult male harvest density from New Hampshire, 1970–2012.

	Yearling				Fawn			Adult
	Antler		Weight (kg)		Weight (kg)		Fawn:Doe	Male
Year	BD (mm)	Points	Male	Female	Male	Female	Ratio	Harvest/km^2
1970							0.71	0.13
1971							0.71	0.13
1972							0.69	0.12
1973							0.70	0.09
1974	17.1	3.3	51.4				0.70	0.12
1975	16.7	2.8	50.5				0.71	0.14
1976	16.6	3.0	49.0				0.72	0.16
1977	17.7	3.9	50.9				0.70	0.12
1978	15.7	2.8	48.3				0.69	0.09
1979	17.1	3.1	48.3				0.72	0.09
1980							0.76	0.10
1981							0.78	0.11
1982							0.72	0.08
1983							0.85	0.07
1984							0.91	0.10
1985							0.90	0.13
1986							0.85	0.15
1987	17.3	3.2	53.9	45.4	28.4	27.0	0.65	0.14
1988	17.0	3.0	52.8	44.9	30.6	29.0	0.73	0.15
1989	17.6	3.1	50.6	43.9	29.9	27.9	0.80	0.18
1990	17.7	3.2	53.0	44.1	30.4	27.9	0.79	0.18
1991	18.3	3.5	54.1	44.6	30.0	27.0	0.75	0.21
1992	17.0	3.1	50.4	44.0	29.4	26.7	0.72	0.23
1993	17.1	3.3	51.1	44.7	29.6	27.4	0.78	0.23
1994	16.9	3.2	53.8	45.0	29.6	27.7	0.72	0.21
1995	17.9	3.6	52.0	42.6	29.9	27.5	0.87	0.26
1996	17.2	3.2	50.2	44.4	31.0	27.4	0.79	0.25
1997	17.1	3.1	51.2	44.7	31.1	27.4	0.68	0.27
1998	18.1	3.5	54.1	45.5	31.2	28.3	0.67	0.22
1999	17.8	3.7	52.9	46.3	30.7	28.2	0.67	0.24
2000	17.1	3.3	51.8	43.6	29.6	27.2	0.61	0.28
2001	17.4	3.3	52.8	44.7	29.2	26.6	0.51	0.26
2002	18.2	3.7	52.0	45.5	32.1	28.3	0.61	0.29
2003	17.3	3.4	53.1	46.3	29.1	27.2	0.58	0.25
2004	17.4	3.0	51.8	45.2	29.4	26.6	0.58	0.24
2005	17.0	3.1	51.2	44.5	29.3	26.3	0.60	0.26
2006	18.2	3.5	53.4	45.1	29.9	26.9	0.66	0.29
2007	17.6	3.2	51.5	43.6	29.1	27.0	0.54	0.33

Table E.3. Biological data from harvested deer, harvest fawn:doe ratio, and adult male harvest density from New Hampshire, 1970–2012.

	Yearling				Fawn			Adult
	Antler		Weight (kg)		Weight (kg)		Fawn:Doe	Male
Year	BD (mm)	Points	Male	Female	Male	Female	Ratio	Harvest/km^2
2008	16.9	3.0	50.5	43.7	29.2	26.6	0.44	0.28
2009	17.4	3.1	51.4	45.4	30.3	28.0	0.46	0.26
2010	18.3	3.5	52.8	45.2	31.5	28.7	0.54	0.26
2011	18.3	3.5	53.1	42.9	28.4	25.8	0.55	0.28
2012	18.2	3.4	51.7	43.4	30.2	27.2	0.47	0.29

Table E.4. Biological data from harvested deer, harvest fawn:doe ratio, and adult male harvest density from Vermont, 1985–2012.

	Yearling				Fawn			Adult
	Antler		Weight (kg)		Weight (kg)		Fawn:Doe	Male
Year	BD (mm)	Points	Male	Female	Male	Female	Ratio	Harvest/km^2
1985							0.71	0.31
1986							0.60	0.30
1987							0.65	0.25
1988							0.60	0.27
1989							0.64	0.33
1990							0.58	0.33
1991							0.66	0.41
1992							0.71	0.40
1993							0.63	0.42
1994							0.49	0.37
1995	16.9	3.0	51.3				0.50	0.46
1996	16.6	2.8	49.7					0.41
1997	16.8	2.9	50.9				0.44	0.43
1998	17.1	3.0	51.3				0.41	0.44
1999	16.9	3.0	52.6				0.32	0.39
2000	16.6	2.9	51.1				0.28	0.42
2001	16.2	2.8	51.9					0.31
2002	17.5	3.1	51.8				0.25	0.36
2003	17.0	2.9	52.0				0.25	0.29
2004	17.0	3.1	51.9				0.21	0.23
2005[1]							0.19	0.16
2006[1]							0.18	0.25
2007[1]							0.19	0.29
2008	16.7	2.8	52.3	45.7	29.3	27.4	0.18	0.30
2009	16.4	2.8	53.7	45.9	28.8	27.1	0.18	0.25
2010	17.2	3.1	54.5	46.3	30.8	27.8	0.18	0.28
2011	16.3	2.6	53.6				0.20	0.24
2012							0.17	0.26

[1] Biological data from 2005-2007 were excluded due to an antler point restriction which protected many yearling bucks from harvest. Beginning in 2008, biological data was collected during the youth season, when the antler point restriction did not apply.